MALACOLOGIA, 1991, 33(1–2): 71–178

THE GENITALIC, ALLOZYMIC AND CONCHOLOGICAL EVOLUTION OF THE TRIBE MESODONTINI (PULMONATA: STYLOMMATOPHORA: POLYGYRIDAE)

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ABSTRACT

The Mesodontini, Tryon, constitute a conchologically diverse radiation of 42 species of land snails in eastern temperate North America. The last monograph on the Mesondontini appeared 50 years ago, and was based primarily on shells.

Dissection of the uneverted penial tubes of all 42 known species revealed a morphological diversity that was classified into five characters comprising 37 character-states. Starch-gel electrophoresis of pedal tissue detected 95 alleles among 16 loci. Maximum-parsimony cladistic analyses, with *Ashmunella* and *Allogona* as outgroups, were performed, assigning weights of 1, 2, 3, 4, 5 and 6 to the genitalic character-states relative to the allozymic character-states. Branch-by-branch visual comparison of all resulting trees resulted in a synthetic phylogenetic hypothesis. Two alternative approaches to phylogenetic analysis closely corroborated this hypothesis, and indicated a basic congruence of anatomical and biochemical data sets.

Supraspecific revision based on this phylogenetic hypothesis divides the Mesodontini into ten genera and subgenera: *Fumonelix* gen. nov.; *Inflectarius* (*Hubrichtius*) subgen. nov.; *I.* (*Inflectarius*) Pilsbry, 1940; *Mesodon* (*Akromesodon*) subgen. nov.; *M.* (*Aphalogona*) Webb, 1954; *M.* (*Appalachina*) Pilsbry, 1940; *M.* (*Mesodon*) Férussac, 1821; *Patera* (*Patera*) Albers, 1850; *P.* (*Ragsdaleorbis*) Webb, 1954; and *P.* (*Vesperpatera*) subgen. nov.

Genitalic and geographic comparisons between 29 pairs of sister taxa detected evolutionary trends similar to those previously found in the Triodopsini: sister taxa with peripatric geographical ranges generally showed little or no difference in penial sculpture; those with sympatric ranges showed no more than moderate differences; and all examples of great genitalic differences, as well as most examples of moderate genitalic differences, between sister taxa occurred in those with parapatric or allopatric ranges. Population-level comparisons for 16 species failed to find any trace of reproductive character displacement with species of similar size and shell shape. These findings support and generalize the hypotheses made for the Triodopsini, that peripheral isolates generally do not differentiate, that differentiation due to reproductive character displacement is moderate at most, and that major differentiation is rare, rapid, and occurs in isolates. These findings do not support the hypothesis that vicariant isolates generally differentiate slowly.

The pattern of shell evolution includes the relative conchological stasis of subgenera, with a few intriguing exceptions. A globose, toothless, imperforate, hairless shell-form occurs in all genera, and typifies the most plesiomorphic subgenera of the two most plesiomorphic genera. If this shell form is indeed plesiomorphic for the Mesodontini, then a parietal denticle evolved independently at least four times; and a basal lamella, an exposed umbilicus, and periostracal hairs each evolved at least three times. Hypotheses concerning the functions of these structures remain untested.

The nature and limits of a species in the Mesodontini require further research. For example, there is extreme variation in penial length within and among nominal species, but the effect of this character on gene flow is unknown. The many sympatric convergences in shells between the Mesodontini (subfamily Polygyrinae) and the Triodopsini, Pilsbry (= *Webbhelix, Neohelix, Xolotrema* and *Triodopsis*) (subfamily Triodopsinae) provide naturally replicated experiments in evolutionary morphology.

Key words: snails; evolution; genitalia; allozymes; shells; cladistics; character displacement; convergence.

INTRODUCTION

The family Polygyridae Pilsbry, 1894a, is autochthonous to North American and comprises approximately 260 species currently classified into 17 genera in three subfamilies (Pilsbry, 1940; Webb, 1974; Hubricht, 1985; Richardson, 1986; Emberton, 1988). This paper deals with a presumed monophyletic radiation (see Emberton, 1986) in the subfamily Polygyrinae that has been known as *Mesodon* Férussac, 1821, and is here elevated to the rank of tribe as Mesodontini, Tryon, comprising 42 species in the following ten subgenera and genera: *Fumonelix* gen. nov.; *Inflectarius* (*Hubrichtius*) subgen. nov.; *I.* (*Inflectarius*) Pilsbry, 1940; *Mesodon* (*Akromesodon*) subgen. nov.; *M.* (*Aphalogona*) Webb, 1954b; *M.* (*Appalachina*) Pilsbry, 1940; *M.* (*Mesodon*) Férussac, 1821; *Patera* (*Patera*) Albers, 1850; *P.* (*Ragsdaleorbis*) Webb, 1954b; and *P.* (*Vesperpatera*) subgen. nov.

The Mesodontini are restricted to eastern temperate North America, east of the Great Plains. They are a common, large (shell diameter about 8–40 mm), and sometimes dominant and conspicuous element of the invertebrate faunas of leaf-litter and floodplain habitats. For example, the density of *Mesodon thyroidus* on a floodplain in Illinois was 63,330 snail per hectare, with a standing tissue biomass of 26 kg per hectare, exceeding maximal fish biomass in the most productive river in the state (Foster, 1937). Dead plant material and living herbs and fungi seem to be their chief foods (Pilsbry, 1940), which are digested by presumably endogenous cellulases (Runham, 1975). Mesodontins are eaten by a wide variety of mammals, reptiles, amphibians and insects (references in Emberton, 1986; personal observations), and thus are an important link in the food chain. Large mesodontins are a potential North American source of anti-A agglutinin for typing human blood, as helicid snails now are in Europe (Miles, 1983). Some mesodontins are intermediate hosts to parasites of various game and non-game mammals, some of them lethal (Maze & Johnstone, 1986). Although human meningoencephalitis, which is carried by land snails and can cause paralysis and blindness in humans, is restricted to the tropics, it has been shown experimentally to be transmissible by the (temperate-climate) mesodontin *Mesodon thyroidus* (Say, 1817) (see Schultz, 1982). Were this disease to invade the United States, phylogenetic knowledge of its potential local carriers could be essential to its control.

As in the case of the tribe Triodopsini, Pilsbry (here erected to comprise the genera *Webbhelix*, *Neohelix, Xolotrema* and *Triodopsis sensu* Emberton, 1988), the large size, high density, low vagility and easy markability of the Mesodontini make them favorable subjects for studies in ecology (e.g. Foster, 1937; Solem, 1955; Blinn, 1963; Randolph, 1973; Emberton, 1981, 1986; Asami, 1988a, 1988b) and population genetics [R. K. Selander, personal communication concerning an unpublished study of *Patera roemeri* (Pfeiffer, 1848); Hubricht (1985) and personal observations concerning the six sympatric color-and-banding morphs of *Mesodon altivagus* on Clingman's Dome, Great Smoky Mountains National Park, Tennessee-North Carolina]. Because of their diversity of courtship displays and methods of external sperm exchange, the Mesodontini are good subjects for studies on systems of mate recognition and speciation (Webb, 1947a, 1947b, 1954b, 1968a, 1968b, 1983). The Mesodontini also exhibit numerous cases of sympatric conchological convergences with the Triodopsini (which have brief courtship and internal sperm exchange), and thus offer superb naturally replicated experiments in evolutionary morphology (see Pilsbry, 1940; Solem, 1976; Emberton, 1986, 1988).

The last monograph on the Mesodontini (Pilsbry, 1940) is now 50 years old, and was based primarily on shells. The purposes of this paper are (1) derivation of a phylogenetic hypothesis for the Mesodontini based on male genitalia and allozymes; (2) revision of the Mesodontini above the level of species based on this phylogenetic inference; and (3) analysis of phylogenetic patterns of variation in both genitalia and shell, in order to generate testable hypotheses about the evolutionary processes that produced these patterns.

For this analysis, the species designations of Hubricht (1985) have been followed, except for elevating *Mesodon altivagus* and *M. trossulus* to the status of species, removing *Inflectarius verus* from synonomy with *I. subpalliatus* and synonomizing *Fumonelix clingmanicus* with *F. wheatleyi*. According to this scheme there are 42 species in the tribe Mesodontini.

Genitalic data are presented here for all 42 species. Most of these data are new. The penial morphologies of ten species of the Mesodontini (*Patera appressa, Fumonelix christyi, Mesodon clausus, M. elevatus, I. inflectus, P. kiowaensis, P. pennsylvanica, P. sargentiana, M. thyroidus* and *M. zaletus*) were previously studied by Webb (1954b; 1968a, 1968b, 1983). As noted for the Triodopsini (Emberton, 1988), Webb's figures tend to omit some structural and sculptural detail. In addition, the anatomical distortion sometimes produced by Webb's technique of killing with boiling water and then often crushing the shell can be even more pronounced in mesodontins than in triodopsins, owing to their lack of rigid sculptural elements. The dissective method for studying penial morphology—slitting and pinning open the uneverted penial tube (Emberton, 1988: Fig. 1)—was recommended by Pilsbry (1940) for future revisers but, until this study, had been used for only eight species of mesodontins: four species (*Mesodon elevatus, M. sayanus, M. thyroidus* and *M. zaletus*) by Leidy (1851); one (*Inflectarius subpalliatus*) by Pilsbry (1940); and three (*Patera binneyana, Mesodon clausus* and *P. clenchi*) by Solem (1976). All of these studies included excellent, detailed illustrations, but only one per species, with little or no discussion of intraspecific variation.

Thus, in genital morphology, 28 of the 42 species of mesodontins never had been examined before, and of the 14 that had, none had been examined for individual variation and six had possible distortion or omission of details or both. Limited additional information on penial sculpture was available from Pilsbry's (1940) one or two sections of the penis for each of 17 species of mesodontins (*Patera binneyana, P. clarki, Mesodon clausus, M. elevatus, Inflectarius ferrissi, I. inflectus, Fumonelix jonesiana, P. laevior, I. magazinensis, P. pennsylvanica, P. perigrapta, P. roemeri, P. sargentiana, M. sayanus, M. thyroidus, F. wheatleyi* and *M. zaletus*), as well as from the histological studies of the penes of two species by Cox (1979: *Mesodon zaletus*) and Cookson (1982: *Mesodon thyroidus*).

The value of combining morphological and molecular data for phylogenetic studies has been well reviewed by Hillis (1987). Starch-gel electrophoresis is now a traditional source of molecular data for phylogenetic analysis (Buth, 1984; Hillis, 1987). New electrophoretic data are reported herein for 39 of the 42 species of the Mesodontini. For only one of these species (*Mesodon normalis*) has electrophoretic data previously been published (McCracken & Brussard, 1980, as reevaluated by Emberton, McCracken & Wooden, in preparation).

MATERIALS AND METHODS

Taxa Studied

The following taxa were studied. Taxa are arranged according to this revision, but here alphabetically by genus and by species within each genus.

Fumonelix gen. nov.
    archeri (Pilsbry, 1940)
    christyi (Bland, 1860)
    jonesiana (Archer, 1938)
    orestes (Hubricht, 1975)
    wetherbyi (Bland, 1874)
    wheatleyi (Bland, 1860)
Inflectarius Pilsbry, 1940
  Inflectarius (*Hubrichtius*) subgen. nov.
    downieanus (Bland, 1861)
    kalmianus (Hubricht, 1965)
  Inflectarius (*Inflectarius*)
    approximans (Clapp, 1905)
    edentatus (Sampson, 1889)
    ferrissi (Pilsbry, 1897)
    inflectus (Say, 1821)
    magazinensis (Pilsbry & Ferriss, 1907)
    rugeli (Shuttleworth, 1852)
    smithi (Clapp, 1905)
    subpalliatus (Pilsbry, 1893)
    verus (Hubricht, 1954)
Mesodon Férussac, 1821
  Mesodon (*Akromesodon*) subgen. nov.
    altivagus (Pilsbry, 1900)
    andrewsae Binney, 1879
    normalis (Pilsbry, 1900)
  Mesodon (*Aphalogona*) Webb, 1954b
    elevatus (Say, 1821)
    mitchellianus (Lea, 1838)
    zaletus ("Say" Binney, 1837)
  Mesodon (*Appalachina*) Pilsbry, 1940
    chilhoweensis (Lewis, 1870)
    sayanus (Pilsbry, in Pilsbry & Ferriss, 1906)
  Mesodon (*Mesodon*)
    clausus (Say, 1821)
    sanus (Clench & Archer, 1933)
    thyroidus (Say, 1817)
    trossulus Hubricht, 1966
Patera Albers, 1850
  Patera (*Patera*)
    appressa (Say, 1821)
    clarki (Lea, 1858)
    laevior (Pilsbry, 1940)
    panselena (Hubricht, 1976)
    perigrapta (Pilsbry, 1894b)
    sargentiana (Johnson & Pilsbry, 1892)
  Patera (*Ragsdaleorbis*) Webb, 1954b
    pennsylvanica (Green, 1827)
  Patera (*Vesperpatera*) subgen. nov.
    binneyana (Pilsbry, 1899)
    clenchi (Rehder, 1932)
    indianorum (Pilsbry, 1899)
    kiowaensis (Simpson, 1888)
    leatherwoodi (Pratt, 1971)
    roemeri (Pfeiffer, 1848)

Collections

Principal field work was conducted April–June, 1982, in the eastern United States ("GS" series), and was supplemented by collections from the lower Ohio River Valley in April, 1980, ("H" series) and from the southern Appalachian area in March–June, 1983, ("SC" series). All collections were deposited in the Field Museum of Natural History, Chicago (FMNH). County-level localities, field-station numbers, and FMNH catalog numbers of dissected and electrophoresed voucher material are listed under each species in the systematic review (Appendix 1). Detailed locality data are available from the author upon request or from the FMNH catalog. Snails in each lot were marked individually on their shells: 1, 2, 3, etc. for snails from which tissue samples were taken; and A, B, C, etc. for snails not so sampled. Appendix 1 shows which individual specimens from each lot were dissected, electrophoresed, and illustrated anatomically or conchologically or both.

Additional anatomical materials (total 16 lots) were borrowed from FMNH, from the Academy of Natural Sciences of Philadelphia (ANSP), and from Mr. Leslie Hubricht's private collection (which has been willed to FMNH).

Dissections

The uneverted penial tubes of 203 snails were dissected, and the everted penes of 19 snails were examined, from a total of 96 populations comprising all 42 species of the Mesodontini.

In order to assess qualitatively the variation in penial-morphological characters at the individual, populational and specific levels, multiple dissections and illustrations were made of two populations each of *Mesodon zaletus* and *M. elevatus* wherever they were sympatric. These two species are very similar in size and shape of shell, and Leidy's (1851: plate X, figs. III, V) illustrations of their penial sculpture indicated an essential similarity. The first sympatric locality was a wooded hillside above a creek, 1.5 miles north of the Sherwood post office, Franklin County, Tennessee (GS-104), collected 1 May 1982 by Ken and Ellen Emberton. The shells of *M. zaletus* and *M. elevatus* were so similar at this site that field identification of many individuals was in doubt; the hypothesis that this represented hybridization, however, was rejected based upon electrophoretic evidence—*M. zaletus* and *M. elevatus* were fixed at alternative alleles for six of the 16 loci examined (Mdh-1, Icd, Gd-1, Got-2, Lap, Mpi; see Table 2). Closer examination of the shells also revealed features reliably distinctive of the two species. Population densities were high at this site owing to the presence of a small trash dump. Of the 41 adults collected in two person-hours, six were *M. zaletus* and 35 were *M. elevatus*. The collecting area was small, on the order of 50 square meters; the two species were almost certainly capable of encountering each other. Five individuals of each species were randomly chosen for dissection, illustration and comparison of the male genitalia.

The second locality studied with sympatric *M. zaletus* and *M. elevatus* was "in the vicinity of the shelter in the primitive camping area, McCormick's Creek State Park, Spencer, Owen County, Indiana," collected 1 June 1974 by Glenn Goodfriend. The collection consists of nine adult and four juvenile *M. zaletus* (FMNH 214785) and of nine adult and two juvenile *M. elevatus* (FMNH 214655), although several "adults" of both species were mature in shell only, with their genitalia immature. Neither the collecting area nor the degree of sympatry was recorded for this collection. The two species were much more readily separable by shell morphology at this site than at that in Tennessee.

For interspecific systematic comparisons, at least three adults per species were dissected whenever possible. Because of the limitations of the material, however, three species (*Patera clenchi, P. pennsylvanica* and *Mesodon trossulus*) were represented by only a single dissection each, and nine species (*Inflectarius approximans, Fumonelix archeri, Mesodon chilhoweensis, I. downieanus, P. indianorum, P. kiowaensis, P. leatherwoodi, F. orestes* and *M. sanus*) were represented by only two dissections each. The remaining 30 species were represented by three to 16 dissections each, often with at least three from a single population.

The number of populations dissected per species ranged from one to ten. A single population was dissected of each of the 22 mesodontin species; two populations were dissected of each of 11 of the species (*M. altivagus, P. appressa, I. approximans, M. chilhoweensis, M. clausus, M. elevatus, I. ferrissi, F. jonesiana, P. leatherwoodi, M. mitchellianus* and *I. rugeli*); three populations of two species (*P. laevior, M. thyroidus*); four populations of one species (*I. inflectus*); five populations of two species (*P. binneyana, M. normalis*); six populations of one species (*P. clarki*); seven populations of one species (*F. wheatleyi*); nine populations of one species (*M. zaletus*); and ten populations of one species (*P. perigrapta*). Not all of the populations of *M. zaletus* and *P. perigrapta* were actually dissected; in some the genital morphology was visible on specimens that had everted their penes in the drowning jar.

Comparisons of genitalic anatomies of outgroups of the Mesodontini were made from published illustrations. According to a preliminary phylogenetic analysis of the Polygyridae (Emberton, 1986), the sister group to the Mesodontini consists of a lineage that split into *Polygyra sensu lato* and *Praticolella,* and its next nearest outgroup is *Stenotrema*. Penial-morphological data on *Polygyra sensu lato* were available from Pilsbry (1940), Webb (1950, 1967), Pratt (1981) and Emberton (1986). Data on *Praticolella* were available from Pilsbry (1940), Webb (1967) and Emberton (1986); and data on *Stenotrema* were available from Pilsbry (1940), Archer (1948) and Webb (1948, 1950). More distant outgroups used for comparison were two genera of the subfamily Ashmunellinae, *Ashumunella* Pilsbry & Cockerell, 1899, and *Allogona* Pilsbry, 1939. Genitalic data for *Ashmunella* were taken from Pilsbry (1940) and Webb (1954a); and for *Allogona* from Leidy (1851) and Pilsbry (1940).

For the Mesodontini, one representative dissection per species was illustrated in detail, using a camera lucida. These illustrations were compared for character-state differences, which were grouped into presumably homologous characters (Patterson, 1982; Wagner, 1989). For each character, a phylogeny of its character-states was proposed, based on the criterion of continuity of forms (Hennig, 1966; Wiley, 1981). These phylogenies were polarized by outgroup comparison (Hennig, 1966; Watrous & Wheeler, 1981).

Electrophoresis

Biochemical methods were identical to those used for the Triodopsini (Emberton, 1988). Posterior pedal tissues ("snail tails") were excised from field-activated snails and stored in screw-top cryogenic vials in liquid nitrogen. Horizontal starch-gel electrophoresis followed methods of Selander et al. (1971)

and Shaw & Prasad (1970), as modified by Davis et al. (1981) and by Emberton (1988). Twelve enzyme systems from a wide array of biochemical pathways (Richardson et al., 1986) yielded 16 variable loci: Sordh, Mdh-1&2, Me, Icd, Pgd, Gd-1&2, Sod-1&2, Got-1&2, Pgm, Lap, Mpi and Gpi. Methodological details are given in Emberton (1988: Appendix A).

The electrophoresed material comprised 706 snails from 81 populations representing 38 or 39 species. The three species for which tissue samples were lacking were *F. archeri, I. downieanus* and *F. jonesiana*. The tissue sample for *P. clenchi* was from a single juvenile specimen, the identity of which was necessarily suspect.

All electrophoresed species were represented by at least one population with complete data for all loci. Sixteen species were represented by a single population each (*M. andrewsae, I. approximans, F. christyi, P. clenchi?, M. elevatus, P. indianorum, I. kalmianus, P. kiowaensis, P. leatherwoodi, I. magazinensis, M. mitchellianus, F. orestes, P. pennsylvanica, M. sanus, M. trossulus* and *F. wetherbyi*); nine species were represented by two populations each (*P. binneyana, M. chilhoweensis, I. edentatus, M. normalis, P. panselena, P. roemeri, P. sargentianus, M. sayanus* and *I. subpalliatus*); 11 species were represented by three populations each (*M. altivagus, P. appressa, P. clarki, M. clausus, I. ferrissi, I. inflectus, P. laevior, P. perigrapta, I. rugeli, I. smithi* and *F. wheatleyi*); one species was represented by five populations (*M. thyroidus*); and one species was represented by eight populations (*M. zaletus*). Catalog numbers of the voucher specimens for all electrophoresed populations are given in Table 2 and in the systematic review (Appendix 1).

Of the electrophoresed snails, 140 belonged to a single population (Monte Sano, Alabama) of *Mesodon zaletus* that was used as the control on all gels for both the Mesodontini and the Triodopsini (Emberton, 1988). Eliminating this and five other populations of *M. zaletus* that were analyzed separately (Emberton, 1986; in preparation), the number of snails electrophoresed per population for the 75 populations listed in Table 2 ranged from one to 22, with a mean of 7.1 and a standard deviation of 5.2.

The closest outgroups of the Mesodontini from which comparable electrophoretic material was available were *Ashmunella danielsi dispar* Pilsbry & Ferriss, 1915, of which one population with a sample size of two was electrophoresed, and *Allogona profunda* (Say, 1821), of which one population with a sample size of ten was included in the analysis, using data from Emberton (1988: Table 2).

Data Analysis

Three methods of phylogenetic analysis were used: (1) maximum-parsimony analysis of combined data, with various weights assigned to anatomical over allozymic data, and a consensus tree constructed from the resulting cladograms; (2) maximum-parsimony analysis of combined data, with successive weighting (Farris, 1988); and (3) maximum-parsimony analyses of anatomical and of allozymic data, and Distance-Wagner analyses of allozymic data, with a consensus tree constructed from the weighted resulting trees (Emberton, 1988). The first of these seems the most objective and informative of all available methods (see Discussion), and is the only method presented in the body of the text. The second and third methods were used only for comparison, and are presented in Appendices 2 and 3.

For phylogenetic analysis (first and preferred method), transformations of the genitalic character-states and the allozymic alleles (see Michevich & Johnson, 1976; Buth, 1984; Hillis, 1987; Swofford & Olsen, 1990) were binary-coded as present (1) or absent (0) for each species. *Ashmunella danielsi dispar* and *Allogona profunda*, both of which scored 0 for all genitalic transformations, were used as outgroups. All autapomorphies were deleted, and the data matrix was analyzed using Hennig86 (Farris, 1988), a cladistics program that uses the criterion of Wagner unrestricted parsimony (Kluge & Farris, 1969; Farris, 1983) and that empirically has been found superior to all other currently available programs (Platnick, 1989). Separate analyses were performed using six different weighting schemes, with each genitalic transformation assigned a weight of 1, 2, 3, 4, 5 and 6 times the weight of each allozymic allele. Each analysis used the mhennig* bb* options. The mhennig* option produces one or more preliminary trees by single passes through the data, then applies branch-swapping to them; the bb* option subjects the resulting trees to further branch-swapping, and outputs all trees of the maximal discovered parsimony. A Nelson (1979) strict consensus tree was then calculated from this set of maximum-parsimony trees, using the "nelsen" option of Hennig86. The six analyses were compared visually to identify those clades most robust to assumptions about the relative reliabilities of morphological and electrophoretic data sets (see Hillis, 1987). A general phylogenetic hypothesis for the Mesodontini was constructed from these comparisons, for use in evaluating evolutionary patterns in genitalic and shell morphology.

Patterns of Genitalic Evolution

Patterns of evolution in penial morphology were analyzed by comparing sister taxa (species or terminal clades appearing dichotomously in the general phylogenetic hypothesis). For each of 29 pairs of sister taxa, their difference in penial morphology (judged from the illustrated dissections) was ranked as great, moderate, slight, or none; and the geographical relationship of their ranges was classified as allopatric, sympatric, parapatric, or peripatric (in which one taxon is a small-ranged endemic peripheral to, or isolated within, the much broader range of the other taxon). Geographic ranges were taken from Hubricht (1985), with slight modification based upon collecting results.

The importance of reproductive character displacement was assessed by first dissecting the genitalia of populations of 16 species that were sympatric with another mesodontin species of similar shell size and shape, then by comparing these dissections with additional dissections of populations that were allopatric with the same species.

Patterns of Shell Evolution

To analyze conchological evolution at the generic, subgeneric and species-group levels, a representative shell was chosen for each species and was mounted in its proper position on the general phylogenetic hypothesis. Patterns of change through time were interpreted under the assumptions that the phylogenetic hypothesis was correct, and the shell morphology of each (unknown) ancestor was intermediate to the morphologies of its living descendents. To aid in analyzing shell evolution, and to assist users of this paper in making identifications, a representative shell of each species, whenever available, was illustrated in detail. Two views are shown—in the apertural plane and perpendicular to the apertural plane—that simultaneously display as many important shell features as possible. For most species, the illustrated shell was from the same population of which the genitalia were illustrated.

TAXONOMIC HISTORY

The origin of the generic name *Mesodon* has been outlined by Rosenberg & Emberton (in press). The name *Mesodon* first appeared in Rafinesque (1819: 66) as *Mesodon leucodon*. Both the generic and specific names were nude, however. Férussac [1821: 33 (quarto) or 37 (folio)] listed *Mesodon leucodon* Rafinesque in the synonymy of *Helix* (*Helicodonta*) thyroidus Say, 1817, and listed *Mesodon helicinum* Rafinesque, a manuscript name, in the synonymy of his *Helix* (*Helicodonta*) *knoxvillina,* then a nude name. The first use of *Mesodon* as an available name was that of Rafinesque (1831: 3), who briefly described the genus, thereby making the name available from the time of its appearance in synonymy in Férussac (1821), and included only *Mesodon maculatum* Rafinesque, 1831 (a *nomen dubium*). Thus by the provisions of the International Commission on Zoological Nomenclature (1985) Articles 11e, 50g and 67l, the correct citation for the genus is *Mesodon* Férussac, 1821, with type species *Helix thyroidus* Say, 1817, by monotypy.

Martens (1860) later expanded *Mesodon* to include all eastern North American land snails with capacious, subglobose shells with a small parietal tooth or toothless, thereby distinguishing it from *Triodopsis* Rafinesque, 1819, in which he included all eastern North American species with depressed, bidentate or tridentate shells (see Pilsbry 1940: 790). Martens' (1860) diagnoses of *Mesodon* and *Triodopsis* were followed by Tryon (1867), Binney & Bland (1869), and some later authors, although many later authors (e.g. Baker, 1939) continued to synonymize the two genera under the genus *Polygyra* Say, 1818. The description of *Polygyra* seemingly had been overlooked by Martens and other European workers.

Pilsbry's (1930) dissections, leading to his monograph on *Mesodon* (Pilsbry, 1940: 702–778), were the first clearly to characterize *Mesodon* anatomically and to recognize it as occupying the entire range of shell shapes also occupied by *Triodopsis* and *Allogona* Pilsbry,

1939. Pilsbry divided *Mesodon* into four subgenera, *Mesodon s. str.* Férussac, 1821; *Patera* Albers, 1850; *Appalachina* Pilsbry, 1940; and *Inflectarius* Pilsbry, 1940, based upon shell shape.

Taxonomic changes in *Mesodon* following Pilsbry's (1940) monograph have been summarized by Miller et al. (1984) and by Richardson (1986). Additional species were described by Hubricht (1954, 1965, 1966, 1975, 1976) and Pratt (1971). Additional distributional records and a few life-history notes were published by several workers, primarily in the journals *Sterkiana* and *Nautilus*, but scattered among many journals and regional faunal surveys. Webb (1954b, 1968a, 1968b, 1983) published a series of reports on the reproductive behavior and everted genitalia of selected species of the Mesodontini, and pointed out important variations in penial morphology, upon which he based his new section *Aphalogona* Webb, 1954b, and subgenus *Ragsdaleorbis* Webb, 1954b.

Solem's (1976) "Comments on Eastern North American Polygyridae" laid solid groundwork for future revision of the Mesodontini. In that work, Solem compared the sympatric, conchologically similar *Patera binneyana, Mesodon clausus* and *Patera clenchi* with one another and with two sympatric, conchologically similar species of the Triodopsini. He compared shell, radular structure, jaw structure, external aspect of the reproductive system and dissected penial morphology, he emphasized the need for comparisons of sympatric species to establish criteria for distinguishing allopatric species, and he indicated penial morphology as potentially the best source of systematically useful characters. Using SEM, Solem detected ectocones on the marginal and lateral radular teeth of *Mesodon clausus,* which had been missed by Pilsbry (1940: 703).

Hubricht's (1985) book of range maps for land snails of the eastern United States made species-level taxonomic changes within the Mesodontini, resulting in a total of 40 species, but did not mention supraspecific taxa. Richardson's (1986) bibliographic catalog of polygyrid species went to press too early to incorporate Hubricht's taxonomic changes.

Concerning the name of the family to which the Mesodontini belong, the International Commission on Zoological Nomenclature has recently been petitioned (Emberton, 1989a) to grant precedence of Polygyridae Pilsbry, 1894a, over Mesodontidae Tryon, 1866, because of its long and stable usage.

RESULTS

Genitalic Analysis

Variation A mesodontin snail copulates by placing its sperm mass on the everted penis of its mate, usually with the two penes intertwining (Fig. 1). The penis (Fig. 2) bears a terminal, ventrally opening, cup-like chalice (Webb, 1954b) for molding the sperm mass; lateral pilasters for containing the sperm mass and often—by differences in their lengths or rigidities—for coiling the penis; and sometimes dorsal ridges or other frictional sculpture for retaining the received sperm mass. The basin of the chalice usually has a lining of minute, parallel riblets that presumably increase the surface area for resorbing water to concentrate and solidify the autosperm mass. Although there is some degree of preservational distortion of the chalice walls in the uneverted penial tube, the structure of the chalice can be studied effectively by dissection (Emberton, 1988: Fig. 1) [e.g., compare Figs. 2 and 11b; compare Figs. 17, 4a–e, 6a–c; and compare Webb (1954b: fig. 6) and Solem (1976: fig. 6b)]. The term chalice is used here in a broader sense than in Webb (1954b), in that all mesodontins are considered to have a chalice, even in cases in which its walls are simply unmodified terminal extensions of the lateral pilasters, and even in those cases in which the chalice is everted during copulation, and thus resembles a glans rather than a basin.

Figure 3, which illustrates the unopened, uneverted penial tubes of five randomly selected *Mesodon zaletus* and five randomly selected *M. elevatus* from a site of sympatry in Tennessee, shows that individual variation is greater than interspecific differences in penial length, penial shape, vas deferens length and retractor-muscle length: the species cannot be separated by these characters.

Figure 4 shows these same ten penial tubes, in the same order, cut open to reveal their sculptural details. Both *M. zaletus* and *M. elevatus* have right and left lateral pilasters, dorsal, longitudinal ridges of variable number and distribution, and thick chalice walls forming a Λ-shaped cleft, with the right chalice wall thicker than the left. In all these characters individual variation exceeds inter-

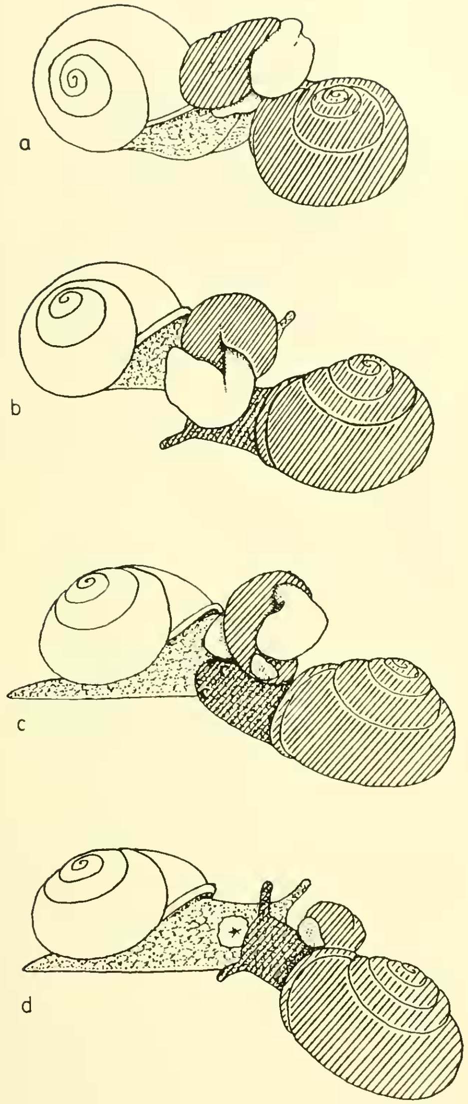


FIG. 1. External sperm exchange in *Mesodon normalis*. a,b. Intertwining of fully everted penes. c. Deposition of sperm mass on mate's penis. d. Inversion of penes and their attached sperm masses.

specific variation. The only consistent differences in penial sculpture between *M. zaletus* and *M. elevatus* of GS-104 that are readily detectable are: the right chalice wall of *M. zaletus* is more thickly and more abruptly swollen than that of *M. elevatus;* the left chalice wall of *M. zaletus* is extended into a slight lateral flap that is lacking in *M. elevatus;* and the surface texture of the right pilaster differs, bearing tiny pock-marks in *M. zaletus,* but bearing angled folds in *M. elevatus.* Even these differences can be difficult to detect in individual cases; *M. elevatus* #39 (Fig. 4i), for example, could easily be mistaken for *M. zaletus* because of local distortion in its chalice walls; and *M. zaletus* #12 (Fig. 4c) is also confusing because its penial tube was inadvertently opened from the ventral side rather than from the dorsal side as in all the other dissections.

Figure 5 diagrammatically illustrates dissections of three randomly chosen specimens of *M. zaletus* and three randomly chosen specimens of *M. elevatus* from another site of sympatry in Indiana, with the unopened, uneverted penial tubes shown *in situ.* As in *M. zelatus* and *M. elevatus* from Tennessee, individual variation in penial size and shape easily outweighs any difference between species (the same is true of the length of the vas deferens, not shown in Figure 5). Another possible difference between the species—the relative points of insertion of the penial retractor muscle and what seems to be the cephalic aorta (also shown diagrammatically in Figure 5)—proved also to be invalidated by individual variation. Although the muscle and artery generally occur closer together in *M. zaletus* than in *M. elevatus,* in some specimens of *M. zaletus* (e.g. #A, Fig. 5a) they are just as far apart as in *M. elevatus.*

Penial sculptures of *M. zaletus* and *M. elevatus* sympatric at the Indiana site are shown in Figure 6, in which four of the six dissected penes (*M. zaletus* #B, D; *M. elevatus* #B, C) are those shown undissected in Figure 5. As in the case of specimens from the Tennessee site, the two species (Fig. 6) have similar right and left lateral pilasters, dorsal longitudinal ridges of variable pattern, and thick chalice walls forming a Λ-shaped cleft. Also as in the previous comparison, the two species differ in that the right chalice wall of *M. zaletus* was more thickly and abruptly swollen than that of *M. elevatus,* and the left chalice wall of *M. zaletus* was extended into a lateral flap lacking in *M. elevatus.* The difference between *M. zaletus* and *M. elevatus* in the surface texture of the right chalice wall and upper right pilaster detected in the Tennessee populations (Fig. 4) is lacking, however, in the Indiana population (Fig. 6). The radically different appearance of *M. elevatus* #B from the

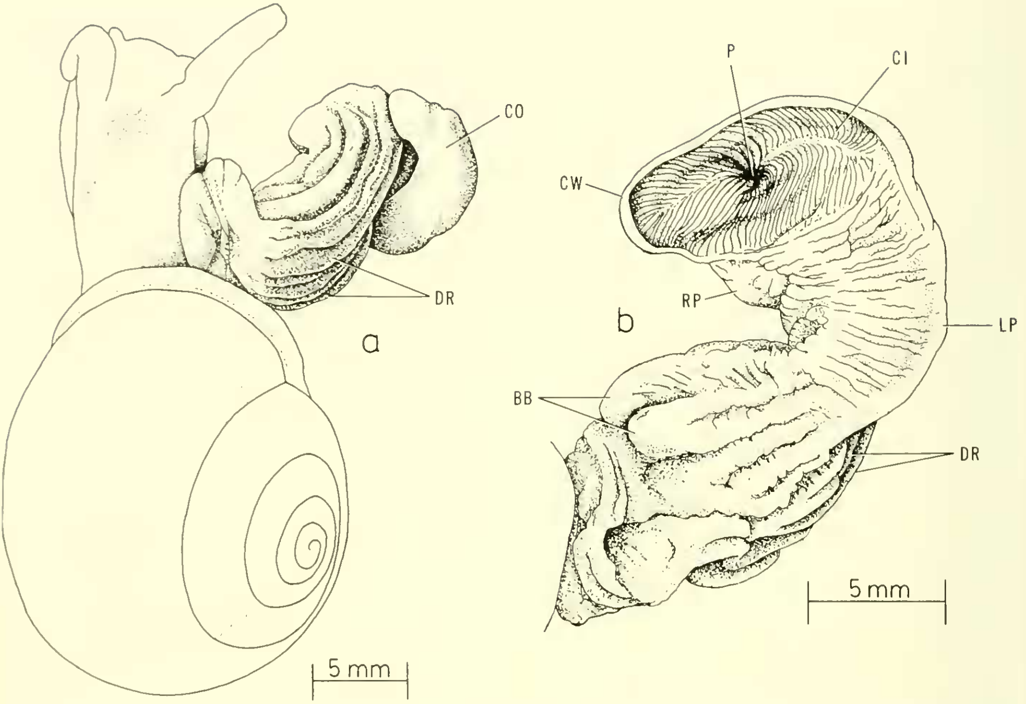


FIG. 2. Dorsal and ventral views of fully everted penis of *Mesodon andrewsae* (GS-11 #2), showing major structural features. BB = basal bulge, CI = chalice inside, CO = chalice outside, CW = chalice wall, DR = dorsal ridge, LP = left pilaster, P = pore = exit of vas deferens, RP = right pilaster.

Indiana site (Fig. 6e) is due to its having been opened from the ventral rather than the dorsal side; this difference emphasizes the importance of using standardized dissecting methods for making anatomical comparisons of this type.

Comparison of *M. zaletus* from the Tennessee with Indiana populations (Fig. 4, top; Fig. 6, top) showed no populational difference greater than individual variation, except for the difference between pock-marked and smooth right chalice walls, as mentioned above. Interpopulational differences in *M. elevatus,* on the other hand, are more pronounced: the Indiana population has chalice walls more nearly equal in size, fewer and less variable dorsal ridges, and a less corded surface structure of the right chalice wall.

Thus the result of these individual, populational and specific comparisons of *M. zaletus* and *M. elevatus* (Figs. 3–6) was to eliminate much of the variation in penial morphology from phylogenetic analysis. The characters that seem to be relatively stable are the overall structures of the lateral pilasters, of the chalice and of the dorsal ridges and bulges. Similar conclusions were drawn from unillustrated comparisons among many populations of other species, especially *Patera binneyana, P. clarki* and *Fumonelix wheatleyi.*

Even without individual and artificial variation, the dissected mesodontin penis, the major features of which are shown in Figure 4 (compare with Figure 2), is moderately rich in sculptural variation useful for phylogenetic analysis. The lateral pilasters, although somewhat inconspicuous in the everted penis (Figs. 2, 17, 20, 23, 24), are easily visible in the dissected, uneverted penis (compare Figure 2 with Figure 11b; the everted with the uneverted portions of the penis in Figure 23; Figure 20a with Figure 20b; Figure 17 with Figures 4a–e, 6a–c).

The relative sizes and shapes of the lateral pilasters seem to be fairly stable within any given species. These pilasters are usually continuous with, or in some way connected to, the walls of the chalice. For the purpose of description and analysis, however, the lateral pilasters and the chalice have been treated as

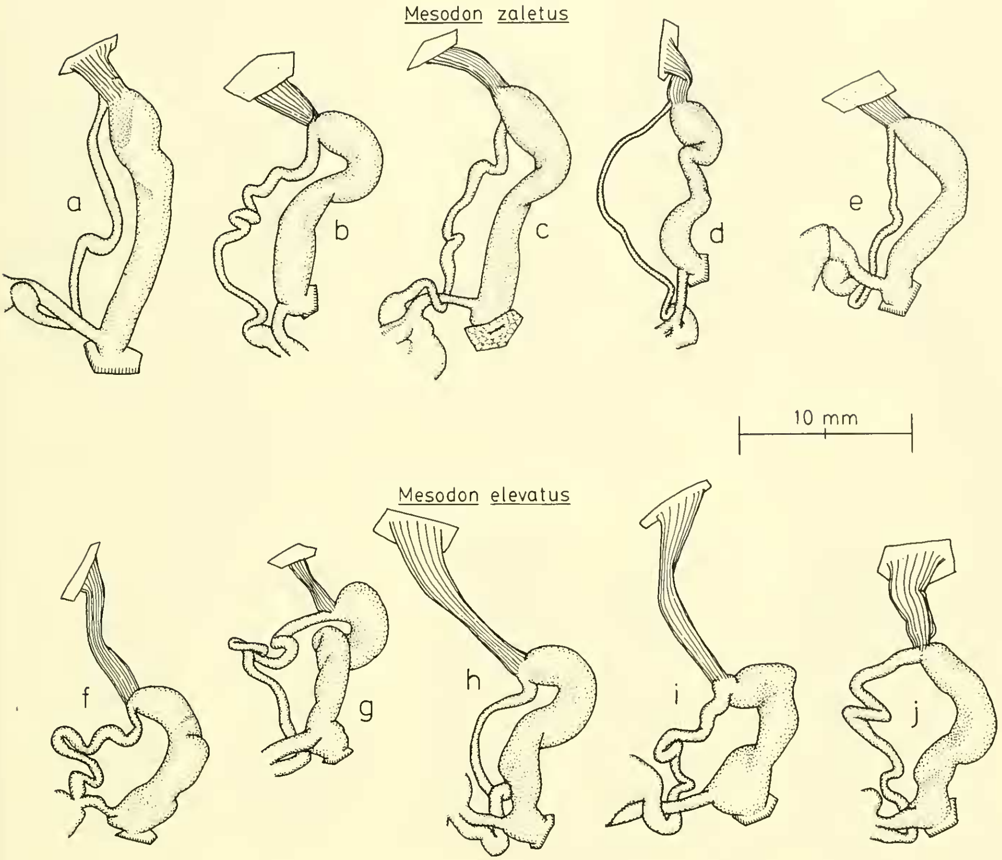


FIG. 3. Uneverted penial tubes of two *Mesodon* species sympatric at GS-104 (Tennessee). a–e. *Mesodon zaletus* #2, 6, 12, 21, 27 f–j. *Mesodon elevatus* #16, 14, 29, 39, 11.

independent characters, because, although there is some correlation between the two, they are usually discrete, and because treating them as a single character would have caused unnecessary complication. In the descriptions below, the convention has been followed of labeling the pilasters and the chalice walls "right" and "left" according to their positions in the illustrated dissections, even though these sides are reversed in the everted, functioning penis. In a few of the dissections, these directional conventions were reversed or confused by opening the penial tube from the ventral rather than the standard dorsal side. All such cases are noted in the labels or in the figure captions.

Descriptions Measurements in the following genitalic descriptions are taken solely from the illustrations (Figs. 4–25) and do not in any way reflect natural variation. [See Emberton (1989b) for an analysis of sources of individual variation in penial length.] Penial length was measured from the apex to the vaginal opening; very curved penes (e.g. *I. ferrissi*) were measured with a Minerva curvimeter from illustrations. Penial width was measured as the distance between the outside edges of the lateral pilasters in the middle region of the penis.

Fumonelix archeri Pilsbry, 1940. (Fig. 7) Dissections: two from one population. Length 13.4 mm, width 2.0 mm. Left lateral pilaster thick (0.5 mm), solid, running full length of penis; at three-fourths of distance from penial apex merging dorsally with right lateral pilaster, expanding to width of 0.9 mm just before merging; at about mid-length of penis, branching ventrally to form left arm of ventral,

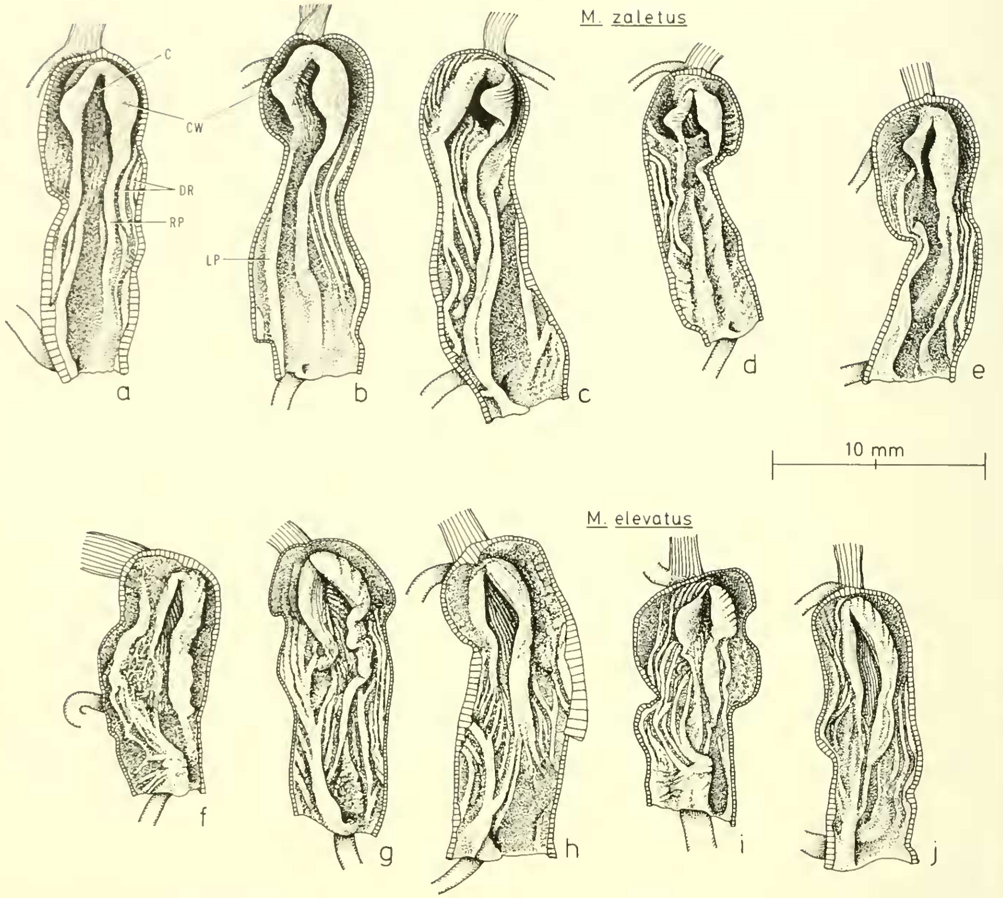


FIG. 4. Opened penial tubes of two *Mesodon* species sympatric at GS-104 (Tennessee). a–e. *Mesodon zaletus* #2, 6, 12, 21, 27. f–j. *Mesodon elevatus* #16, 14, 29, 39, 11. Same specimens and in same order as in Figure 3. C = chalice, CW = chalice wall, DR = dorsal ridge, LP = left pilaster, RP = right pilaster. All were opened from dorsal side except for c, which was opened from ventral side.

V-shaped pouch or notch. Right lateral pilaster solid, cord-like, variable in width but generally narrow (0.2 mm) in its mid-region and expanding apically (to 0.7 mm) to its junction with right chalice wall and basally (to 0.6 mm) to its merger with left lateral pilaster. Basal pilaster (formed by fusion of lateral pilasters) situated on basal 3.9 mm of penis, massive, solid, 1.3 mm wide and with narrow notch apically, gradually tapering to 0.4 mm wide basally. Ovate ventral bulge, 1.1 mm long and 0.6 mm wide, present on right side of ventral surface of penis at about its mid-length. On left side of ventral surface, adjacent to ventral bulge, is a V-shaped ventral notch composed of right and left, short (2.0 mm) cord-like or fold-like arms, originating from just above ventral pilaster and from branch of left lateral pilaster, respectively, and meeting in sharply acute angle. Ejaculatory pore flush with penial wall. Chalice walls relatively thick (ca. 0.5 mm) and firm, apical wall high (2.0 mm) and basally pocket-shaped, forming pointed, symmetric hood over chalice. Penial walls free of other structures.

Fumonelix christyi (Bland, 1860). (Fig. 8a) Dissections: three from one population. Length 8.6 mm, width 1.9 mm. Left lateral pilaster short (ca. 2.2 mm long) and thin (ca. 0.05 mm wide). Right lateral pilaster stretching nearly entire length of penis (length 7.7 mm), narrow throughout (width 0.05 mm), basally connected with dorsal bulge by oblique ridge. Right side of dorsal surface of penis

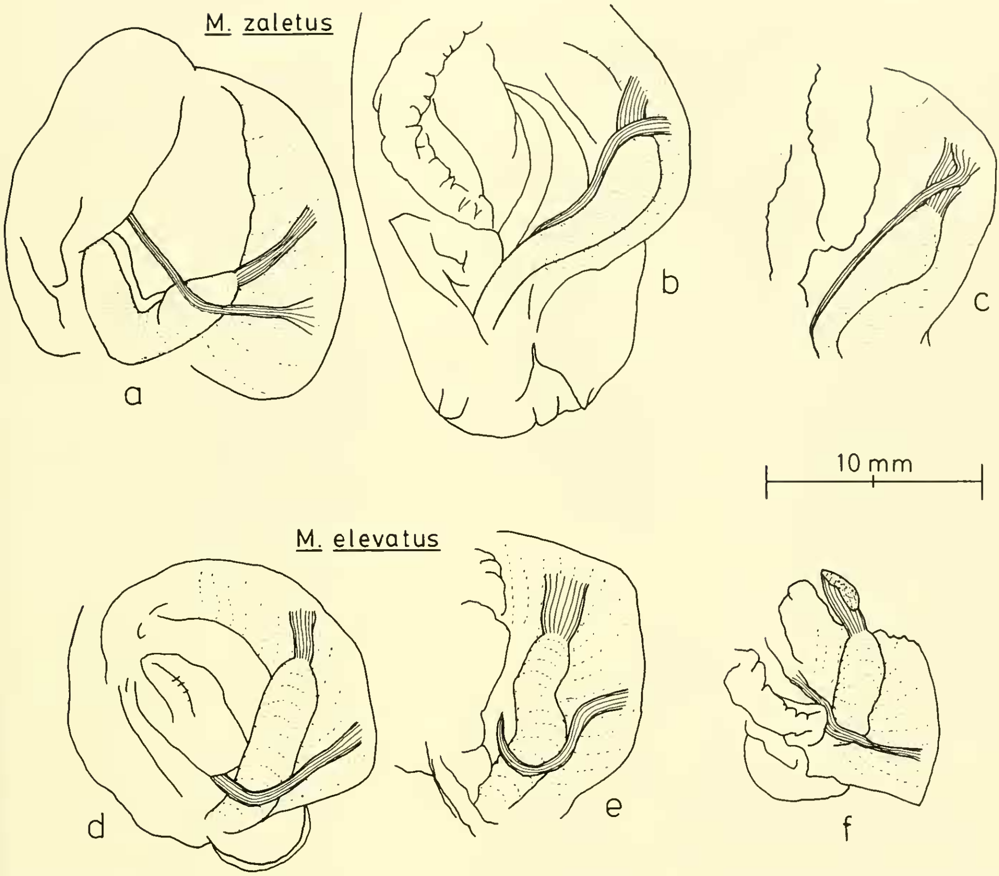


FIG. 5. Penial retractor muscle and cephalic aorta in two *Mesodon* species sympatric at McCormick Creek, Indiana. a–c. *Mesodon zaletus* #A, B, D. d–f. *Mesodon elevatus* #B, C, D.

bearing pilaster-like bulge, thick (0.6 mm), massive, firm and long (4.2 mm), ending about 1.4 mm above base of penis, tapering to blunt point both apically and basally, in its middle third parallel and very close to right lateral pilaster, but angling slightly away from right lateral pilaster in both its apical and basal thirds, the basal third connected to lower right lateral pilaster by obliquely angled ridge 0.9 mm long and 0.1 mm wide. Ejaculatory pore flush with penial wall. Chalice walls 0.1 mm thick at their edges, continuous with lateral pilasters, and forming basally pointing, moderately deep (0.6 mm), symmetric, rounded hood or cup, 1.1 mm in outside diameter. Penial wall otherwise lacking in structures (the minute ridges and patterns in Figure 8a are seemingly artifacts of preservation).

Fumonelix jonesiana (Archer, 1838). (Fig. 8b) Dissections: five from two populations (including topotypes). Length 14.7 mm, width 2.6 mm. Left lateral pilaster 0.6 mm wide, rounded, firm, extending about 3.5 mm from its juncture with left side of left chalice wall to its effacement in penial wall just above ventral bulge. Right lateral pilaster low and nearly obsolete, 5.3 mm long and 0.6 mm wide, narrowing basally. Penis dominated by firm, massive ventral bulge, 8.5 mm long, 1.0 mm wide apically, swelling basally to width of 2.1 mm, occupying usual position of basal portion of left lateral pilaster, but seemingly neither continuous nor homologous with it. Ejaculatory pore flush with wall of penis. Chalice cup-shaped, 1.8 mm in diameter, ca. 1.2 mm deep, and with edges ca. 0.3 mm thick, rim continuous for four-fifths of the circumfer-

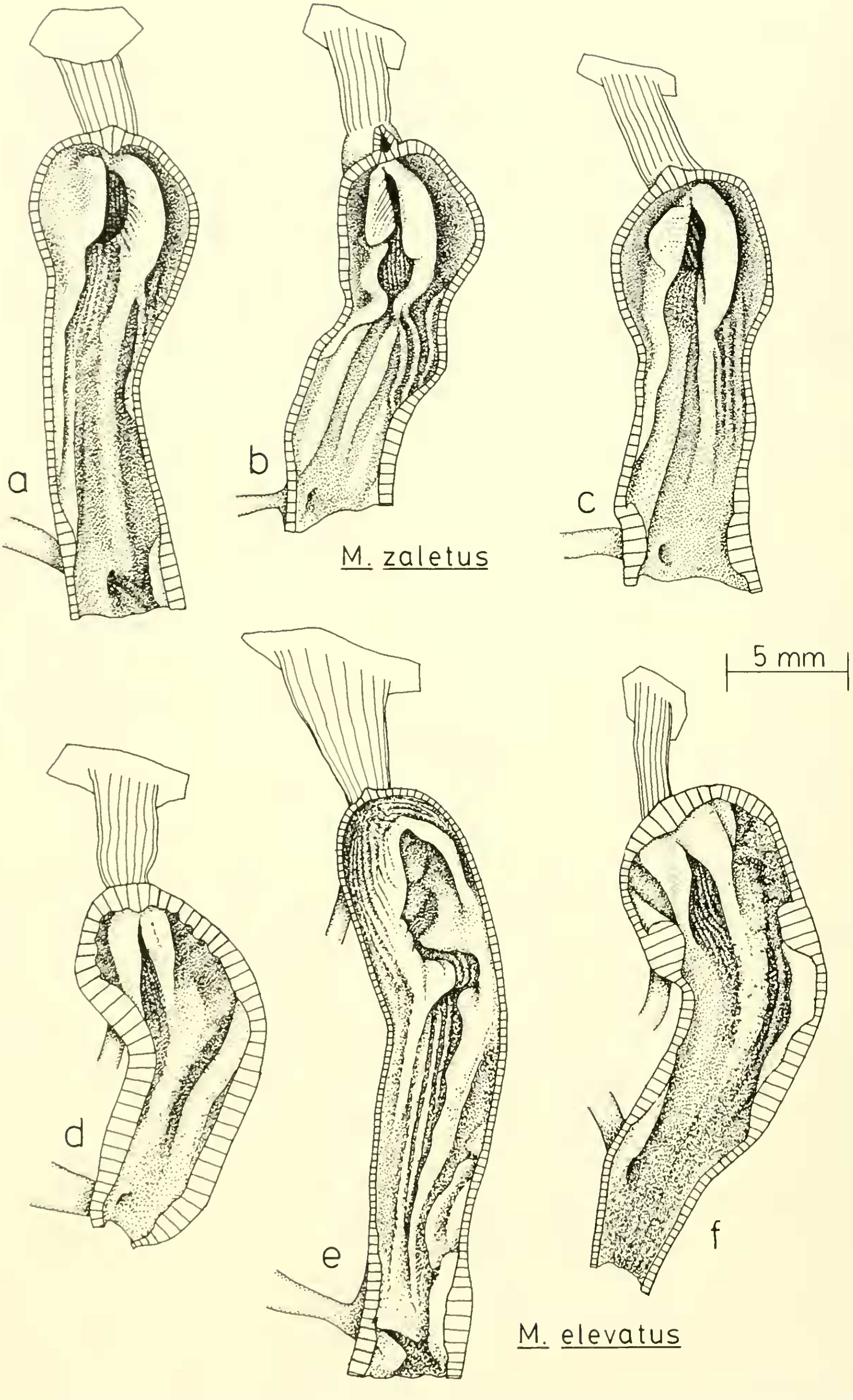


FIG. 6. Opened penial tubes of two *Mesodon* species sympatric at McCormick Creek, Indiana. a–c. *Mesodon zaletus* #B, C, D. d–f. *Mesodon elevatus* #A, B, C. Nearly the same specimens and ordered as in Figure 5. All were opened from dorsal side except for e, which was opened from ventral side.

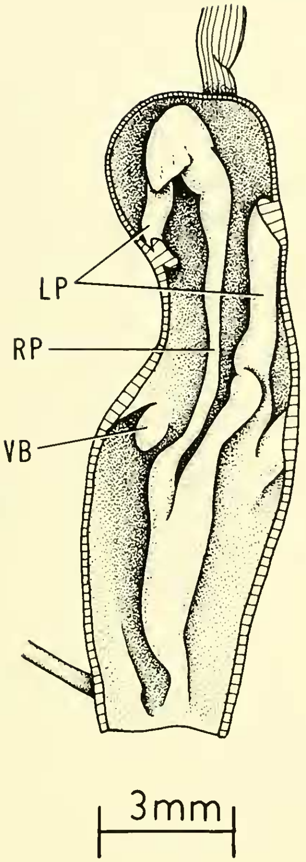


FIG. 7. Opened uneverted penial tube. *Fumonelix archeri*, SC-279 #A (also dissected #B). LP = left pilaster, RP = right pilaster, VB = ventral bulge.

ence, lower or missing on basal side. Penial walls otherwise free of structures (the thin ventral connections between the lateral pilasters, as well as the dark rugosities on the left dorsal wall, in Figure 8b, are seemingly preservational artifacts).

Fumonelix orestes Hubricht, 1975. (Fig. 8d) Dissections: two from one population (topotypes). Length 15.0 mm, width 3.0 mm. Left lateral pilaster apically firm, cord-like, and widening from 0.2 mm at its inception on left side of chalice to 0.5 mm near midpoint of penis, below which, after possible hiatus, it is uniformly broad (0.5 mm) and flattened against penial wall. Right lateral pilaster also extending full length of penis, firm, cord-like, gradually widening, with a possible hiatus near the midpoint of the penis, from 0.3 mm at chalice to 0.6 mm at base of penis, possibly turning dorsally to approach left lateral pilaster near its base. Ventro-basal penial wall bearing a massive, firm, fleshy bulge, somewhat teardrop-shaped, length 2.4 mm, greatest width 1.4 mm. Ejaculatory pore flush with wall of penis. Chalice shaped like hood of a cloak, its walls relatively thick (0.2 mm) and firm, ca. 1.8 mm across and 1.1 mm deep. Penial walls without other sculpture.

Fumonelix wetherbyi (Bland, 1874). (Fig. 9b) Dissections: four from one population. Length 13.6 mm, width 3.0 mm. Left lateral pilaster a humped ridge, ca. 0.3 mm thick at its edge, 4.3 mm long from its point of merger with left chalice wall, ca. 0.8 mm maximal height near its midpoint. Right lateral pilaster extending full length of penis, rather thin (0.2 mm?), extremely high-standing, and in uneverted penis recurved to right to form tube 1.1 to 0.6 mm in diameter. Ejaculatory pore flush with wall of penis. Chalice walls thin and high-standing, forming deep, cylindrical cup; in uneverted penis, chalice walls are buckled and folded inward, falsely appearing thicker and more massive. Penial walls seemingly otherwise free of other structures (the fine basal ridges and basal nodular folds of the right lateral pilaster seem to be preservational artifacts).

Fumonelix wheatleyi (Bland, 1860). (Fig. 8c) Dissections: 15 from seven populations. Length 6.0 mm, width 1.3 mm, expanded apically. Right and left lateral pilasters difficult to discern, but seemingly thickned bands (width ca. 0.2 mm) along right and left sides of middle third of penis. Just dorsal to apices of lateral pilasters and just below and to sides of chalice, are two bulges, 1.1 mm long and 0.3 mm wide, longitudinally oriented. At base of penis, just above opening of vagina, is a medially placed, longitudinally oriented ventral bulge, 1.5 mm long and 0.6 mm wide. Ejaculatory pore seemingly flush with penial wall. Chalice walls firm, fixed in shape, forming basally-opening, spherical hood or cup 1.0 mm in diameter, its opening ca. 0.4 mm wide. Penial walls otherwise smooth (I interpret the folds, or bands, between the ventral and apico-lateral bulges as artifacts).

Inflectarius (*Hubrichtius*) *downieanus* (Bland, 1861). (Fig. 10a) Dissections: two from one population; specimens had been placed live into isopropanol, so were highly retracted. Length 3.8 mm, width 1.3 mm. Left lateral pilaster sausage-shaped, 1.8 × 0.5 mm, lower end bluntly rounded, upper and tapering rapidly into chalice wall. Left pilaster somewhat

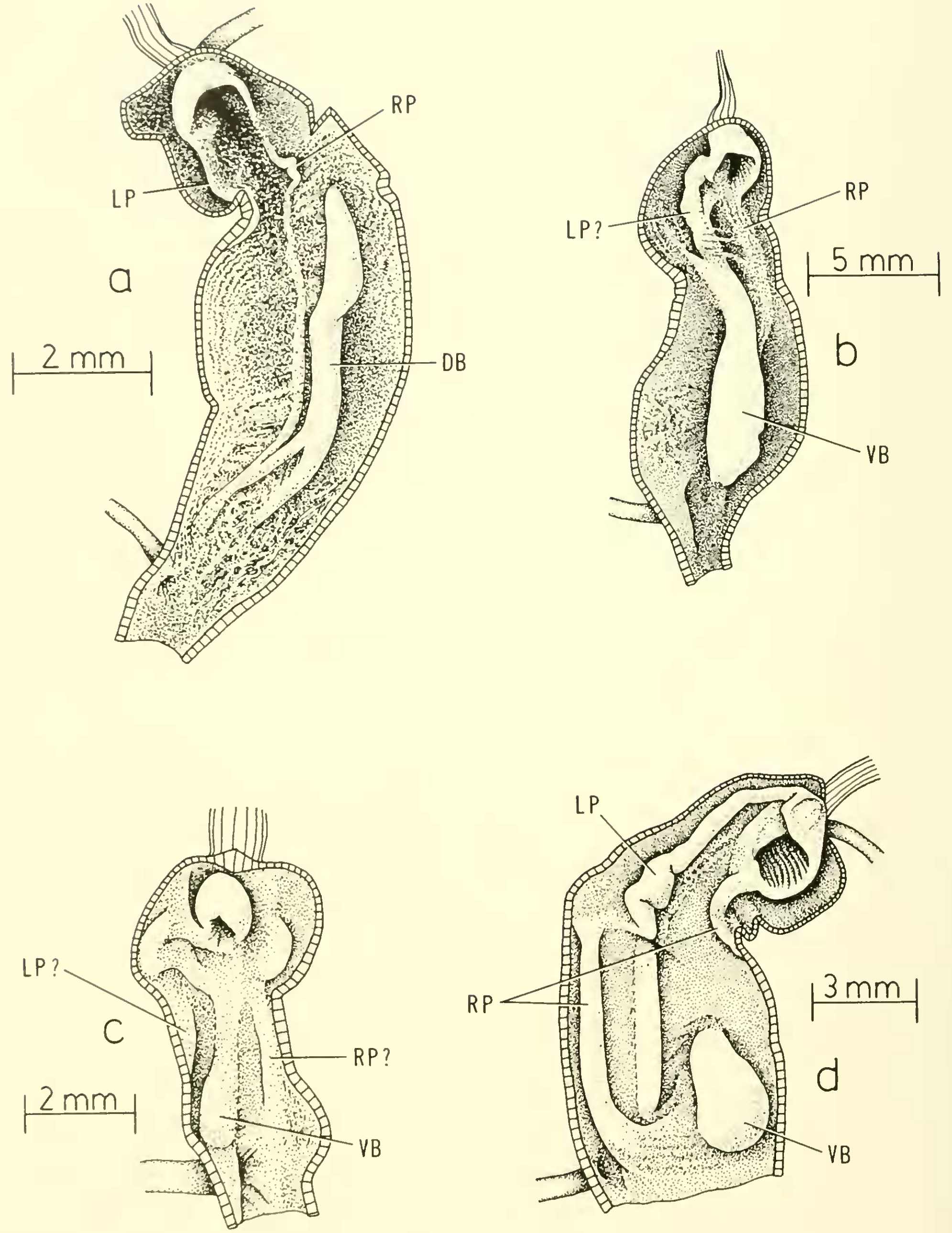


FIG. 8. Opened uneverted penial tubes. a. *Fumonelix christyi* GS-161 #6. A sperm mass adhered to the pilaster. (Also dissected #2, 5.) b. *Fumonelix jonesiana,* SC-155 #5 (also dissected #4, 9). c. *Fumonelix wheatleyi,* GS-6 #5 [also dissected #1, 3; GS-10 #2, 9, 12; GS-153 #4, 7, 10; SC-144 (subspecies *clingmanica*) #1, 2; SC-192 #3; SC-202 #1, 2; SC-212 #2. Populations differ in length, in size and position of bulges and in whether main pilaster is divided.] d. *Fumonelix orestes,* GS-86 #4 (also dissected #2). DB = dorsal bulge, LP = left pilaster, RP = right pilaster, VB = ventral bulge.

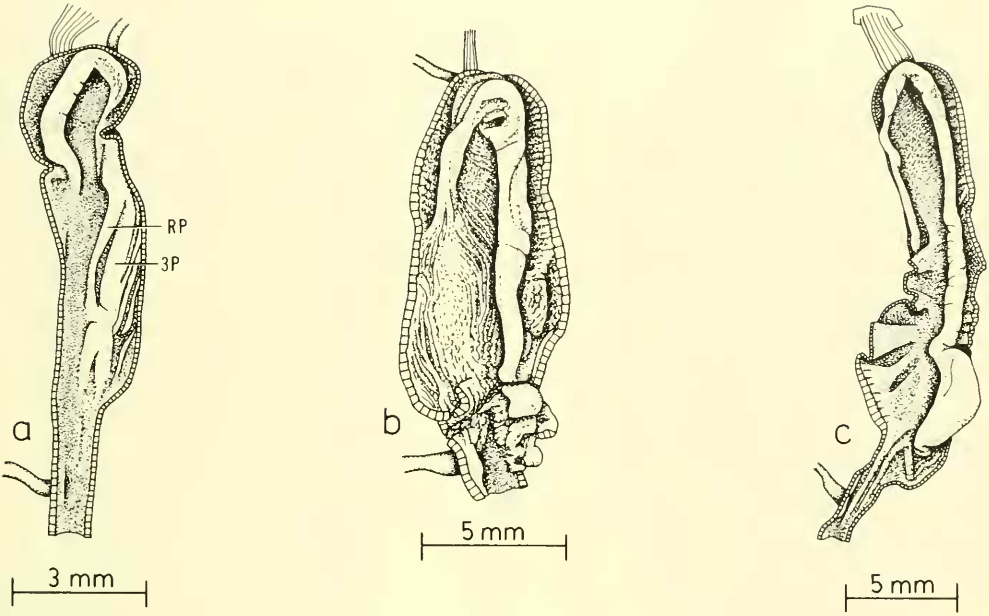


FIG. 9. Opened uneverted penial tubes. a. *Inflectarius inflectus,* SC-130 #2 (also dissected #3, 8; GS-16 #21, 27, 29; GS-95 #1; SC-26 #A). b. *Fumonelix wetherbyi,* GS-115 #20 (also dissected #1, 2, 7). Chalice actually a high-standing, thin-walled cup, with its base surrounding opening of vas deferens; in illustrated specimen, chalice walls are buckled and folded inward. Main pilaster very high and thin, and rolled over to left (ca. 1/4 turn here) in all specimens examined. c. *Inflectarius smithi,* GS-101 #4 (also dissected #1, 2). RP = right pilaster, 3P = third pilaster.

rhomboidal with thin, rounded edge, slightly pendant below, 1.1 × 0.4 mm; trace of a low, simple, ridge-like right lateral pilaster, 0.2–0.1 mm wide, runs rest of length of penis. Ejaculatory pore flush with penial wall. Upper chalice wall thick (0.2 mm) and high-standing, widening rapidly right and left into continuity with lateral pilasters. Penial wall free of other structures.

Inflectarius (*Hubrichtius*) *kalmianus* Hubricht, 1965. (Fig. 11a) Dissections: four from one population. Length 6.9 mm, width 0.9 mm, slightly expanding apically. Left lateral pilaster extending along apical half of length of penis, width 0.2 mm basally, gradually widening to 0.3 apically before flaring slightly as left wall of chalice. Right lateral pilaster seemingly extending full length of penis, thin (less than 0.1 mm) and inconspicuous basally, gradually widening apically to about 0.3 mm before continuously grading into right chalice wall. Ejaculatory pore flush with penial wall. Chalice walls soft, seemingly erectile, high-standing, right higher than left. Penial walls free of other structures (the small ridge- and pustule-like patterns shown in Figure 11a are seemingly preservational artifacts).

Inflectarius (*Inflectarius*) *approximans* (Clapp, 1905). (Fig. 12a) Dissections: two from two populations. Length 5.7 mm, width 2.0 mm. Right and left lateral pilasters both extending entire length of penis, left one massively larger than right. Upper two-thirds of left pilaster cylindrical, 0.8 mm wide; lower third tapering to 0.2 mm. Left pilaster ca. 0.1 mm wide. Ejaculatory pore flush with penial wall. Chalice undifferentiated, seemingly a continuation of right lateral pilaster. Penial wall free of other structures.

Inflectarius (*Inflectarius*) *edentatus* (Sampson, 1889). (Fig. 12c) Dissections: three from one population. Length 10.0 mm, width 2.1 mm, expanding at tip. Left lateral pilaster short (1.7 mm), broad (0.6 mm), merging into penial wall basally and continuous terminally with chalice wall. Right lateral pilaster running full length of the penis, rounded, gradually widening from 0.2 mm basally to 0.8 terminally. Ejaculatory pore flush with penial wall. Chalice walls thick (0.9 to 1.1 mm), soft, and

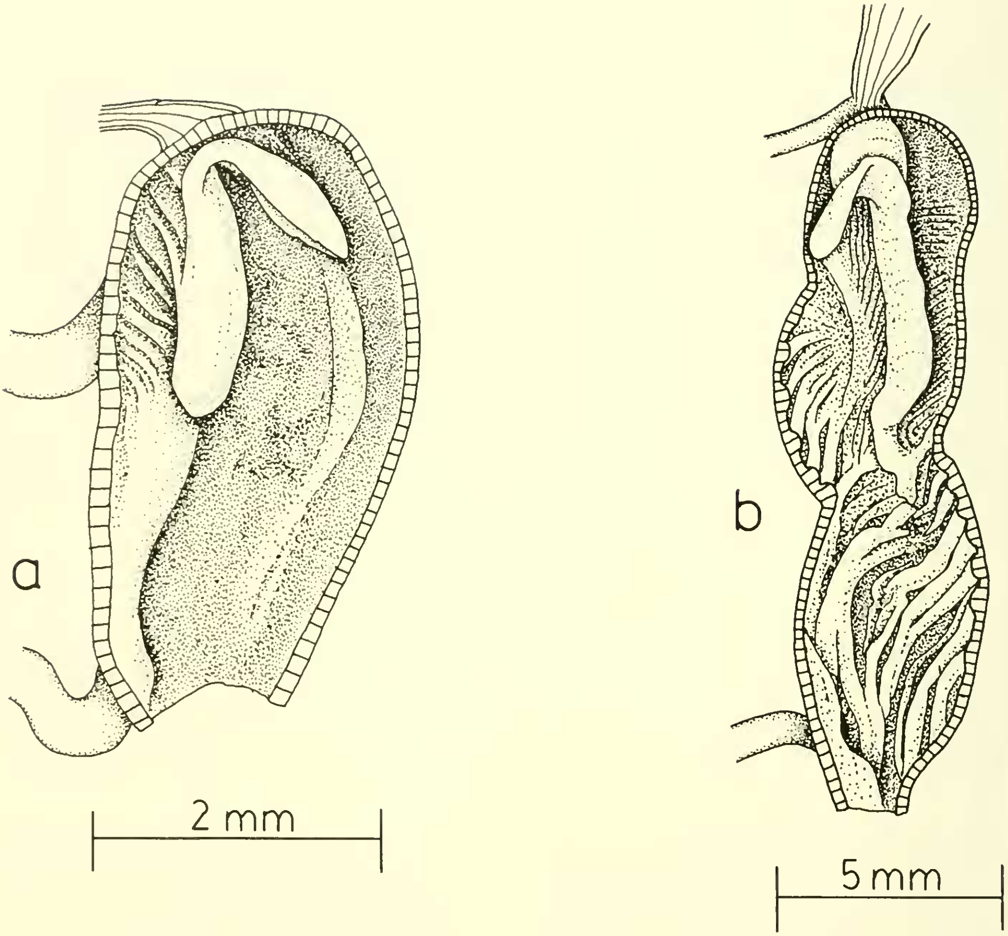


FIG. 10. Opened uneverted penial tubes. a. *Inflectarius downieanus*, Hubricht 30825 #B (also dissected #A; both highly contracted specimens). b. *Patera pennsylvanica*, GS-206 #1.

folded, seemingly composed of erectile tissue. Penial walls free of other adornment (the small ridges and reticulations shown in Figure 12c presumably are preservational artifacts).

Inflectarius (*Inflectarius*) *ferrissi* (Pilsbry, 1897). (Fig. 13c) Dissections: six from two populations (including topotypes). Length 36.4 mm, width 4.0 mm, narrowing apically and basally. Left lateral pilaster running approximately four-fifths length of penis, 0.7 mm wide apically, tapering gradually to less than 0.1 mm wide. Right lateral pilaster running full length of penis, 1.2 mm wide, tapering apically to 0.4 mm before joining chalice. A third pilaster occurs on dorsal surface of penis between lateral pilasters from base of penis to about two-thirds of length of penis apically, tapering in width from 1.7 mm basally to 0.4 mm apically. Chalice uniquely spoon-shaped with firm walls approximately 0.3 mm thick, its "handle" formed by right lateral pilaster, ejaculatory pore in its basin, and seemingly separate from left lateral pilaster. Penial walls free of other structures (the nodular structures and the folds in the third pilaster shown in Figure 13c are seemingly artifacts of preservation).

Inflectarius (*Inflectarius*) *inflectus* (Say, 1821). (Fig. 9a) Dissections: eight from four populations. Length 9.6 mm, width 1.4 mm. Left lateral pilaster solid and massive, running about one-third length of penis (2.5 mm), apically merging with chalice wall, uniformly broad (0.6 mm) for most of length until taper-

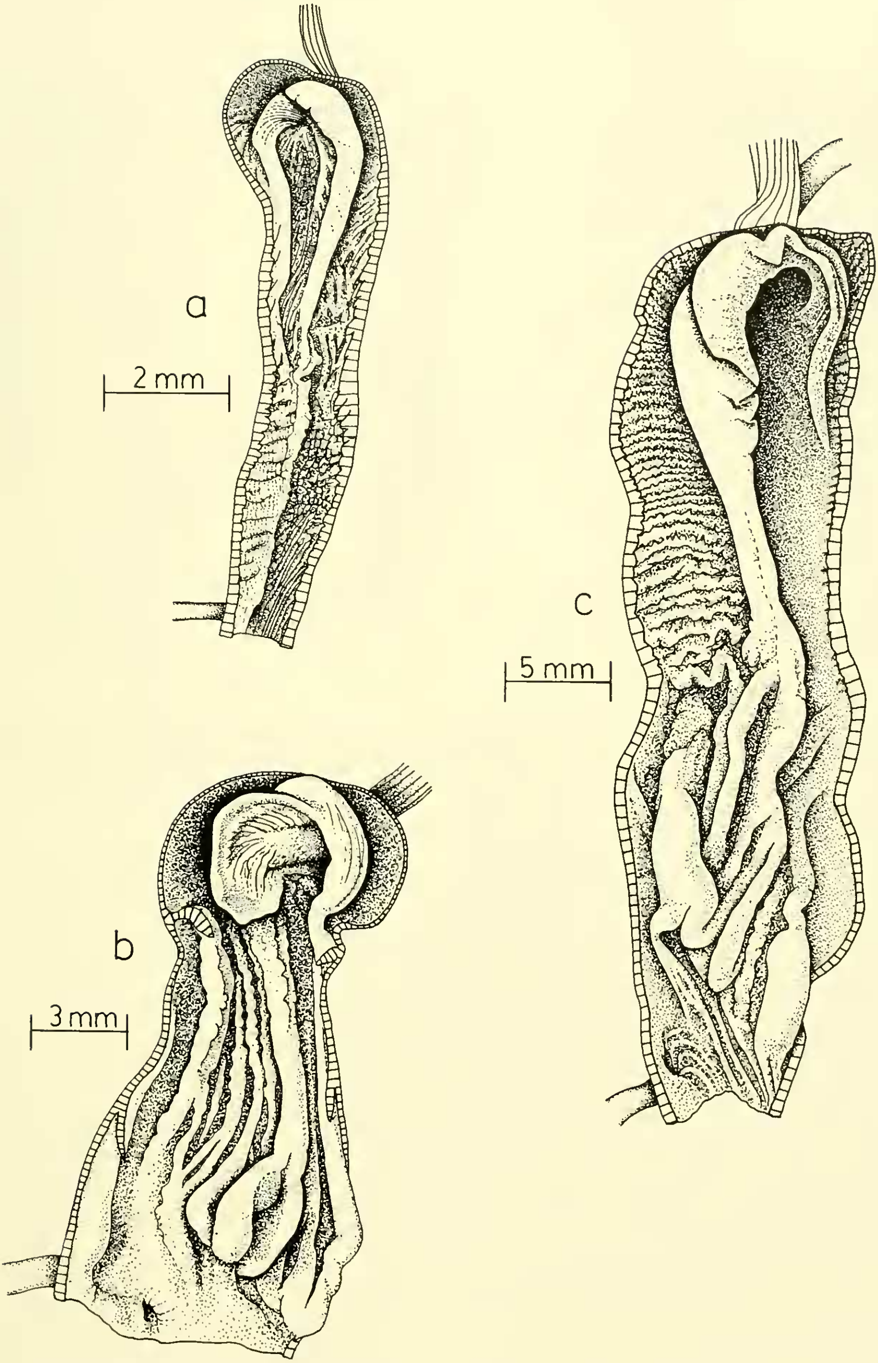


FIG. 11. Opened uneverted penial tubes. a. *Inflectarius kalmianus,* GS-116 #13 [also dissected #A; GS-188 (=GS116) #2, A, the latter with perfectly smooth walls]. b. *Mesodon andrewsae,* Roan Mountain, GS-11 #8 [also dissected #4 and examined #2 (fully everted—see Figure 2) and #3 (3/4 everted)]. c. *Mesodon normalis,* SC-158 (=SC145) #4 (also dissected SC-204 #2, 3; SC-154 #8, 10, 13; SC-184 #5, 6,10; SC-149 #3, 7, 11). This species highly variable in size and shape of chalice.

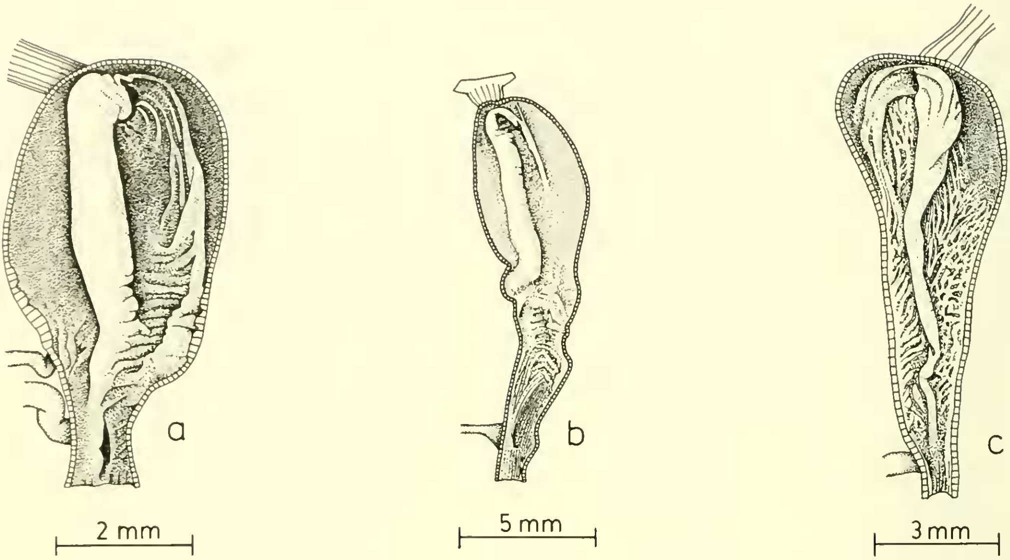


FIG. 12. Opened uneverted penial tubes. a. *Inflectarius approximans,* GS-57 #1 (also dissected Hubricht 23497 #A). b. *Inflectarius magazinensis,* GS-95 #5 (also dissected #6, 14). c. *Inflectarius edentatus,* GS-90 #2 (also dissected #7, 9).

ing basally (to 0.3 mm). Right lateral pilaster running along about middle three-fifths of penis, narrow (0.1 mm) at its midpoint, but widening (0.3 mm) at two positions near its base and its apex where it merges with third pilaster. Third pilaster dorsal to, parallel with, equal in length to, and twice merging with right lateral pilaster; broad (0.4 mm). Ejaculatory pore flush with penial wall. Chalice wall undifferentiated from left lateral pilaster, but on right side broader (0.4 mm) than right lateral pilaster to which it seemingly tapers, and apparently composed of soft, erectile tissue. Remaining penial walls seemingly free of other structures (the small dorsal ridges shown in Figure 9a seem to be preservational artifacts).

Inflectarius (*Inflectarius*) *magazinensis* (Pilsbry & Ferriss, 1907). (Fig. 12b) Dissections: three from one population (topotypes). Length 12.8 mm, width 1.7 mm, apically expanded. Left lateral pilaster extending along upper half of penis, broad (0.9 mm) and massive throughout length, ending abruptly both basally and apically. Right lateral pilaster short (2.6 mm) and narrow (0.2 mm). Ejaculatory pore flush with penial wall. Chalice walls low and solid, about 0.1 mm thick throughout, continuous with, but seemingly well differentiated from, right and left lateral pilasters. Penial walls free of other structures (the basal patterns and the thin apical extension of the right lateral pilaster shown in Figure 12b are presumably artifacts of preservation).

Inflectarius (*Inflectarius*) *rugeli* (Shuttleworth, 1852). (Fig. 13b) Dissections: six from two populations. Length 14.0 mm, width 2.0 mm. Left lateral pilaster extending from 1.6 mm above base of penis to its juncture with left chalice wall, 0.2 to 0.3 mm wide, and branching basally to form pattern of nested, broadly U-shaped ridges. Right lateral pilaster extending to about mid-length of penis from its merger with right chalice wall, 0.3 mm wide. A third pilaster running mid-dorsally from about level of ejaculatory pore into first dorsal U-shaped ridge (total length 7.9 mm), parallel to and separate from lateral pilasters. Ejaculatory pore flush with wall of penis. Chalice walls high-standing, thin-edged, flared to left, composed of soft, presumably erectile tissue. Penial walls free of other structures (other small sculpture shown in Figure 13b is presumably an artifact).

Inflectarius (*Inflectarius*) *smithi* (Clapp, 1905). (Fig. 9c) Dissections: three from one population (topotypes). Length 20.0 mm, width 2.8 mm Left lateral pilaster extending along approximately upper two-fifths of length

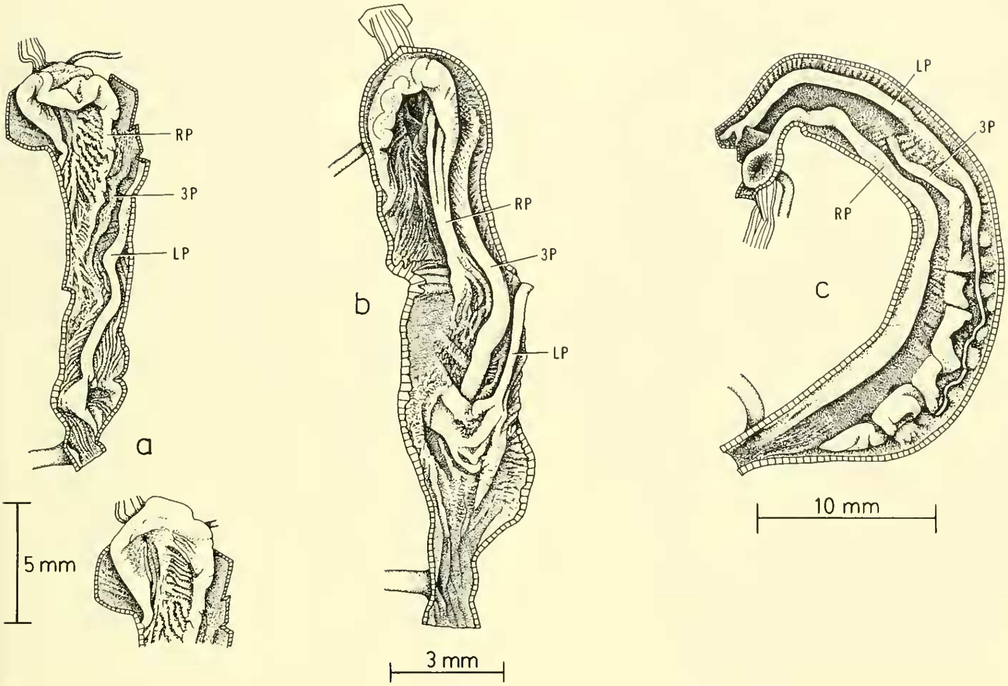


FIG. 13. Opened uneverted penial tubes. a. *Inflectarius subpalliatus*, GS-153 #2 (also dissected #1, 3). b. *Inflectarius rugeli*, SC-130 #2 (also dissected #3, 4; GS-3 #5, 10, A). c. *Inflectarius ferrissi*, GS-5 #3 (also dissected #1, 4; SC-216 #2, 3, 6). LP = left pilaster, RP = right pilaster, 3P = third pilaster.

of penis, 0.3 mm wide throughout, seemingly ending abruptly basally. Right lateral pilaster twice as wide as the left (0.6 mm), uniform in width from its merger with right chalice wall to merger with basal bulge. Basal bulge massive, firm, humped, an extension of right lateral pilaster, 4.4 mm long, 1.4 mm wide, 1.9 mm high at its midpoint, and 1.1 mm high at its ends, ending basally 3.6 mm above base of penis. Ejaculatory pore flush with penial wall. Chalice walls continuous with and slightly higher-standing and thinner than apical lateral pilasters. Penial walls otherwise featureless (the folds and tiny bumps shown in Figure 9c are preservational artifacts).

Inflectarius (*Inflectarius*) *subpalliatus* (Pilsbry, 1893). (Fig. 13a) Dissections: three from one population. Length 16.1 mm, width 1.7 mm, expanding apically. Left lateral pilaster extending entire length of penis, widening basally from 0.2 to 0.5 mm, with local thickenings, rapidly expanding near base of penis on dorsal side to width of 0.9 mm. Right lateral pilaster extending to mid-length of the penis, thin, tapering from 0.2 mm. A third pilaster, of about same size, length (6.5 mm) and vertical position as right lateral pilaster, runs along dorsal surface of penis between and parallel to lateral pilasters, lacking anastomoses with either. Ejaculatory pore flush with penial wall. Chalice walls quite high-standing, thin-edged, composed of flexible, presumably erectile tissue, flared to left. Penial walls free of other structures (the small basal ridges shown in Figure 13a are preservational artifacts).

Inflectarius (*Inflectarius*) *verus* (Hubricht, 1954). (Fig. 14) Dissections: three from one population (topotypes). Length 6.0 mm, width 1.3 mm. Left lateral pilaster merging with left chalice wall so as to be indistinguishable from it, short, tapering basally to point less than one-third length of penis from its apex. Right lateral pilaster extending entire length of penis, uniformly broad (0.5 mm) until tapering in its basal 0.7 mm, with several short (0.3 mm), oblique cord-like buttresses to dorsal penial wall. Ejaculatory pore flush with penis wall. Chalice walls more expanded than lateral pilasters, with which they are continuous, wide on right (0.7 mm), much narrower at apex and

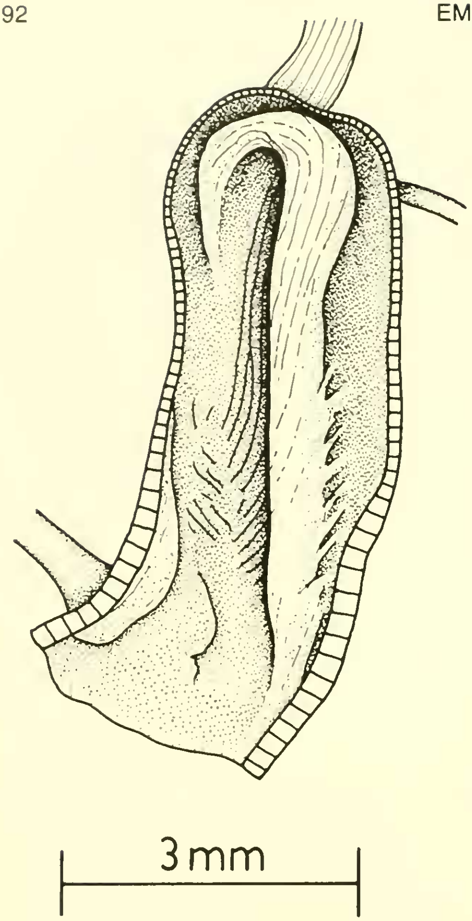


FIG. 14. Opened uneverted penial tube of *Inflectarius verus,* GS-10 #8 (also dissected #3, 4).

on left (0.3 mm). Small, longitudinally oblique, possibly expansive folds occur in chalice walls and lateral pilasters. Penial walls free of other structures.

Mesodon (*Akromesodon*) *altivagus* (Pilsbry, 1900). (Fig. 15c) Dissections: three from two populations. Length 25.4 mm, width 3.9 mm. Left lateral pilaster seemingly extending full length of penis, but not clearly defined owing to its branching into, or proximity to, system of dorsal ridges. Right lateral pilaster extending entire length of penis, solid and cord-like, narrow apically and basally (0.3 mm), irregularly expanded medially (maximal width 1.8 mm), merging branch-like with at least two of dorsal ridges. Upper four-fifths of dorsal penial wall wholly covered by fairly regular pattern of dorsal ridges. Dorsal ridges smooth, solid, cord-like, parallel, longitudinally oblique, meeting right lateral pilaster at angle of about 20 degrees, variously merging with or tapering alongside lateral pilasters, each varying in width, usually broadest medially (0.9 mm) and tapering laterally (to 0.3 mm), but with expanded ridge or section of ridge occurring both apically and basally (maximal widths 1.5 mm). Ejaculatory pore flush with penial wall. Chalice walls thin (0.3 mm), flexible, forming deep (2.1 mm) cup with thickened (0.6 mm), less flexible, conspicuously flared extension of left wall (length 2.4 mm). Basal penial wall with broad, loose fold associated with bases of the dorsal ridges, but otherwise free of additional structures.

Mesodon (*Akromesodon*) *andrewsae* Binney, 1879. (Figs. 2, 11b) Dissections: four from one population (two dissected, two already everted). Length 16.1 mm, width 3.7 mm, expanded basally and apically. Left lateral pilaster thick (0.8 mm), firm, cord-like, extending nearly entire length of penis, apically seemingly distinct from left chalice wall, and in basal fourth thickening and splitting into cluster of three or four basal bulges. Right lateral pilaster solid, cord-like, 0.5 mm wide and 9.8 mm long from point of merger with right chalice wall, branching in lower third to give rise to narrow (0.2 mm) dorsal ridge. Dorsal surface of penis covered with cord-like ridges 0.2 to 0.4 mm in diameter; these run longitudinally, roughly parallel to lateral pilasters and to each other, but in their basal third variously divide or merge both with one another and with basal bulges. Basal bulges each about 3.4 mm long, 1.2 mm wide and 1.0 mm high; one of them is on ventral surface of penis, and differs from dorsal bulges by having apically-directed groove, or pocket. Ejaculatory pore flush with wall of penis. Chalice walls soft, thin-edged (0.2 mm), presumably erectile, high-standing (ca. 2.4 mm), flared to left side. Penial wall otherwise free of structures (the transverse wrinkles on the ventral surface of the everted penis shown in Figure 2b are presumably preservational artifacts).

Mesodon (*Akromesodon*) *normalis* (Pilsbry, 1900). (Figs. 1, 11c) Dissections: 12 from five populations. Length 38.3 mm, width 4.4 mm. Left lateral pilaster extending full length of penis, firm, cord-like, 1.5 mm wide from juncture with left chalice wall to about midpoint of penis, below which it narrows as it gives rise to four or five baso-dorsal bulges. Right lateral pilaster short to absent, indistinguishable from right chalice wall. Lower half to third of dorsal penial wall covered with system of

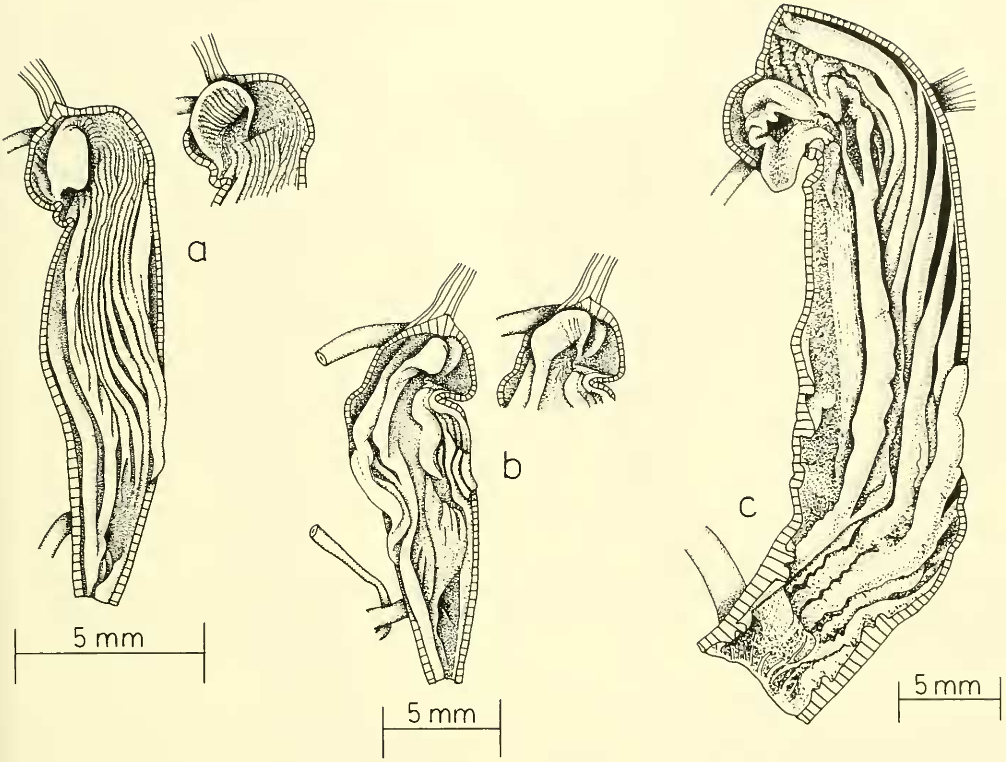


FIG. 15. Opened uneverted penial tubes. a. *Mesodon sanus,* GS-103 #2 (also dissected #1). b. *Mesodon thyroidus* GS-63 #69 [also dissected #1, 8, 14, 18; GS-202 #3; GS-78 (subspecies *bucculentus*) #6, 8, 12]. c. *Mesodon altivagus,* SC-144 #7 (also dissected #9, 10; GS-145 #4).

basal bulges, ranging in shape from ridges (width 0.7 mm, length 3.6 to 9.9 mm) to lumps (diameter 2.6 mm, length 6.2 mm), that variously merge with one another and with base of left lateral pilaster. Ejaculatory pore flush with wall of the penis. Chalice wall relatively thin (ca. 0.3 mm) and flexible, low on right, rapidly expanding to flare highly on left, forming asymmetric scoop that is diagnostic but variable in size and shape. Penial wall otherwise free of structures (the pattern of transverse ridges on the upper dorsal surface and the small longitudinal ridges at the base shown in Figure 11c seem to be preservational artifacts).

Mesodon (*Aphalogona*) *elevatus* (Say, 1821). (Figs. 3f–j, 4f–j, 5d–f, 6d–f) Dissections: eight from two populations. Length: for Tennessee population (n = 5), mean = 12.4 mm, standard deviation = 2.0 mm; for Indiana population (n = 3), mean = 17.1 mm, standard deviation = 4.0 mm. Length: Tennessee mean = 2.2 mm, standard deviation = 0.4 mm; Indiana mean = 2.4 mm, standard deviation = 0.5 mm. Left lateral pilaster extending one-third to two-thirds length of penis, cord-like, ca. 0.3 mm wide at juncture with left chalice wall, tapering to obscurity basally. Right lateral pilaster extending two-thirds to full length of penis, broad (0.5 to 1.0 mm), tapering basally, with substructure of parallel cords. Dorsal penial wall covered with system of about five to ten cord-like ridges about 0.1 mm wide, predominantly longtiduinally parallel, occasionally merging with one another and with lateral pilasters, and sometimes coalescing to form false dorsal pilaster (Fig. 4f). Ejaculatory pore flush with penial wall. Right and left chalice walls meeting apically in V-shaped notch, both usually with substructure of parallel cords; left wall 3.3 mm long, 0.6 mm wide, rounded (Fig. 4h) or slightly flap-like (Fig. 4i), basally tapering gradually (Figs. 4f, j) or rapidly (Fig. 6f); right chalice wall ei-

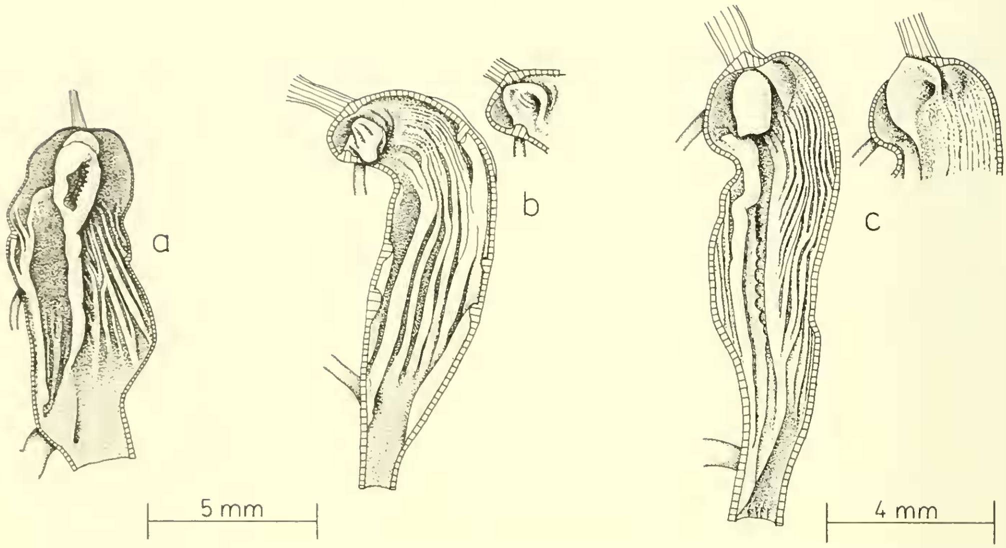


FIG. 16. Opened uneverted penial tubes. a. *Mesodon mitchellianus,* Hubricht 19406 # B (also dissected #A, C; GS-154 #1, 5, 6). b. *Mesodon clausus,* GS-116 #11 (also dissected #6, 17; GS-28 #A, B, C, E). c. *Mesodon trossulus,* GS-53 #3.

ther identical to the left (Fig. 6d–f) or slightly to conspicuously broader (Fig. 4f–j). Penial walls otherwise free of structures. The abnormal appearance of the sculpture shown in Figure 6e is due to the fact that this penial tube was opened from the ventral rather than the standard dorsal side; apical knobs and bulges are artifacts of preservation and folding, the dorsal ridges appear centrally, and the small apical ridges are at the basin of the chalice. The deficiency of sculptural features shown in Figure 6d and, to a lesser extent, in Figure 6f could be due to local variation or could be an artifact due to tight contraction of the penis, as indicated by its thick walls.

Mesodon (*Aphalogona*) *mitchellianus* (Lea, 1838). (Fig. 16a) Dissections: five from two populations. Length 9.0 mm, width 1.7 mm. Right and left lateral pilasters both extending full length of penis and merging ventrally at its base; left pilaster beginning as thin (0.1 mm) arc from lower left side of chalice, continuing as longitudinal cord 0.2 mm wide; right pilaster thick (4.0 mm in diameter) and cord-like in upper three-fifths, angling ventrally and tapering rapidly (to ca. 0.1 mm diameter) in lower two-fifths before joining left lateral pilaster. Dorsal penial wall covered with field of cord-like ridges less than 0.1 mm in diameter, ranging in orientation from longitudinal to a 30-degree slant to left, and variously anastomosing among themselves and with upper left lateral pilaster. Ejaculatory pore opening on summit of fleshy, solid, cylindrical pedestal ca. 0.3 mm high, the sides of which are continuous with chalice. Chalice completely enclosed, deep (ca. 0.9 mm) cylinder with thin, continuous wall (ca. 0.1 mm), right edge of which is scalloped, and basal-most point of which is continuous with right lateral pilaster. Other structures are not evident, although the baso-ventral longitudinal ridges shown in Figure 16a could be real instead of artificial.

Mesodon (*Aphalogona*) *zaletus* ("Say" Binney, 1837). (Figs. 3a–e, 4a–e, 5a–c, 6a–c, 17) Dissections: ten from four populations. Length: for Tennessee population (n = 5), mean = 14.3 mm, standard deviation = 1.5 mm; for Indiana population (n = 3), mean = 16.3 mm, standard deviation = 1.7 mm. Width: Tennessee mean = 1.9 mm, standard deviation = 0.3 mm; Indiana mean = 2.5 mm, standard deviation = 0.4 mm. Left lateral pilaster extending full length of penis, firm, cord-like, 0.3 to 0.6 mm wide, continuous with left chalice wall. Right lateral pilaster extending full length of penis, firm, cordlike, widest (ca. 0.6 mm) just below indistinct junction with right chalice wall, tapering basally to about 0.3 mm wide. Dorsal penial wall bear-

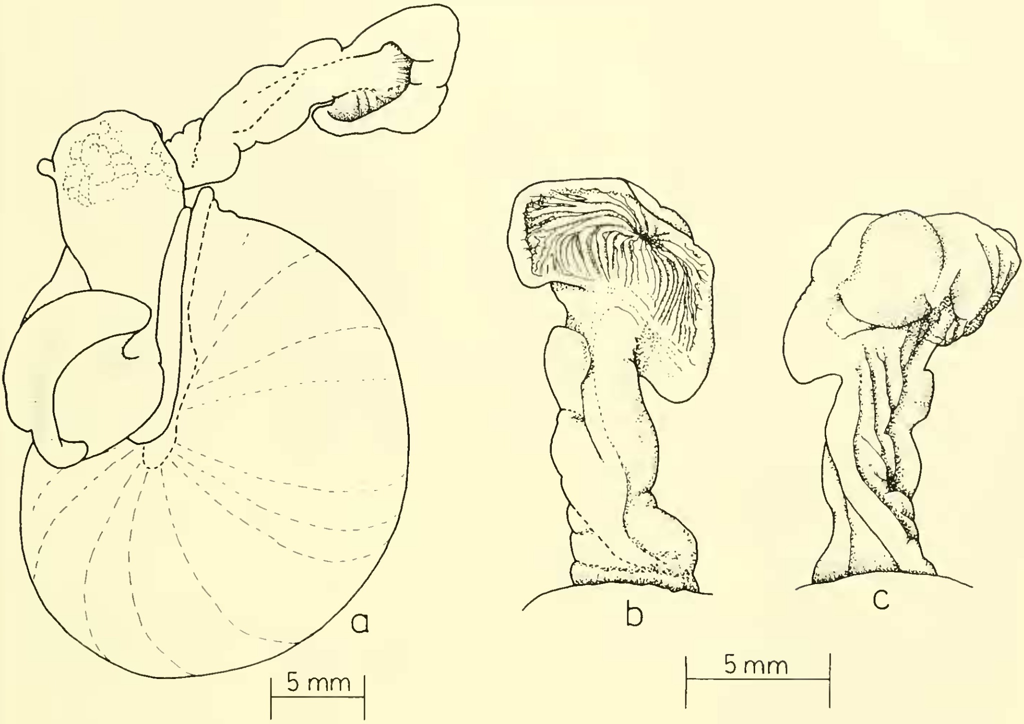


FIG. 17. *Mesodon zaletus,* with fully everted penis, from SC-71. a. Ventral view of whole animal, with body twisted such that head is in dorsal view but apex of penis is in ventral view. b. Ventral view of penis, uncoiled and with chalice pinned open. c. Dorsal view of same.

ing approximately four cord-like ridges, ca. 0.1 mm wide, approximately parallel, and oriented either longitudinally or at a slight angle so as to merge with either or both of lateral pilasters. Ejaculatory pore flush with penial wall. Right and left chalice walls distinct, meeting apically in V-shaped notch; left wall thick (ca. 0.4 mm), firm, 2.7 to 4.2 mm long, at midpoint drawn into conspicuous flap, 1.2 to 1.5 mm high; right wall thicker (ca. 0.7 mm), massive, usually bulging in central region or just below. Penial wall otherwise free of sculpture. The dissection shown in Figure 4c seems unusual because the penial tube was opened from the ventral side instead of the standard dorsal side, hence the dorsal ridges are in the center, and the sides are reversed.

Mesodon (*Appalachina*) *chilhoweensis* (Lewis, 1870). (Fig. 18b) Dissections: two from two populations. Length extreme: 203.7 mm, of which apical, basal, and middle regions totalling 38.7 mm are shown in Figure 18b. Width 3.3 mm. Left lateral pilaster stretching entire length of penis, 0.7 mm wide in apical and basal regions, 0.4 mm wide in mid-regions, rounded, cord-like. Right lateral pilaster extremely short, perhaps absent, indistinguishable from right chalice wall. Ejaculatory pore flush with penial wall. Chalice walls rather thin (0.3 mm) and firm, higher-standing on left (2.0 mm) than on right (at most 1.0 mm), fairly even in height on each side. Penial walls seemingly free of other structures (the apical folds, basal nodules and the transverse ridges throughout all seem to be artifacts of preservation).

Mesodon (*Appalachina*) *sayanus* (Pilsbry, in Pilsbry & Ferriss, 1906). (Fig. 18a) Dissections: three from one population. Length 20.2 mm, width 2.0 mm. Left lateral pilaster short (ca. 2.0 mm) and narrow (ca. 0.2 mm), tapering rapidly from left chalice wall, with which it is continuous. Right lateral pilaster extending perhaps two-thirds of length of penis, 0.2 to 0.3 mm wide, becoming inconspicuous basally. Ejaculatory pore flush with wall of the penis. Chalice wall evenly high on left (ca. 0.7 mm), apically diminishing to become low on

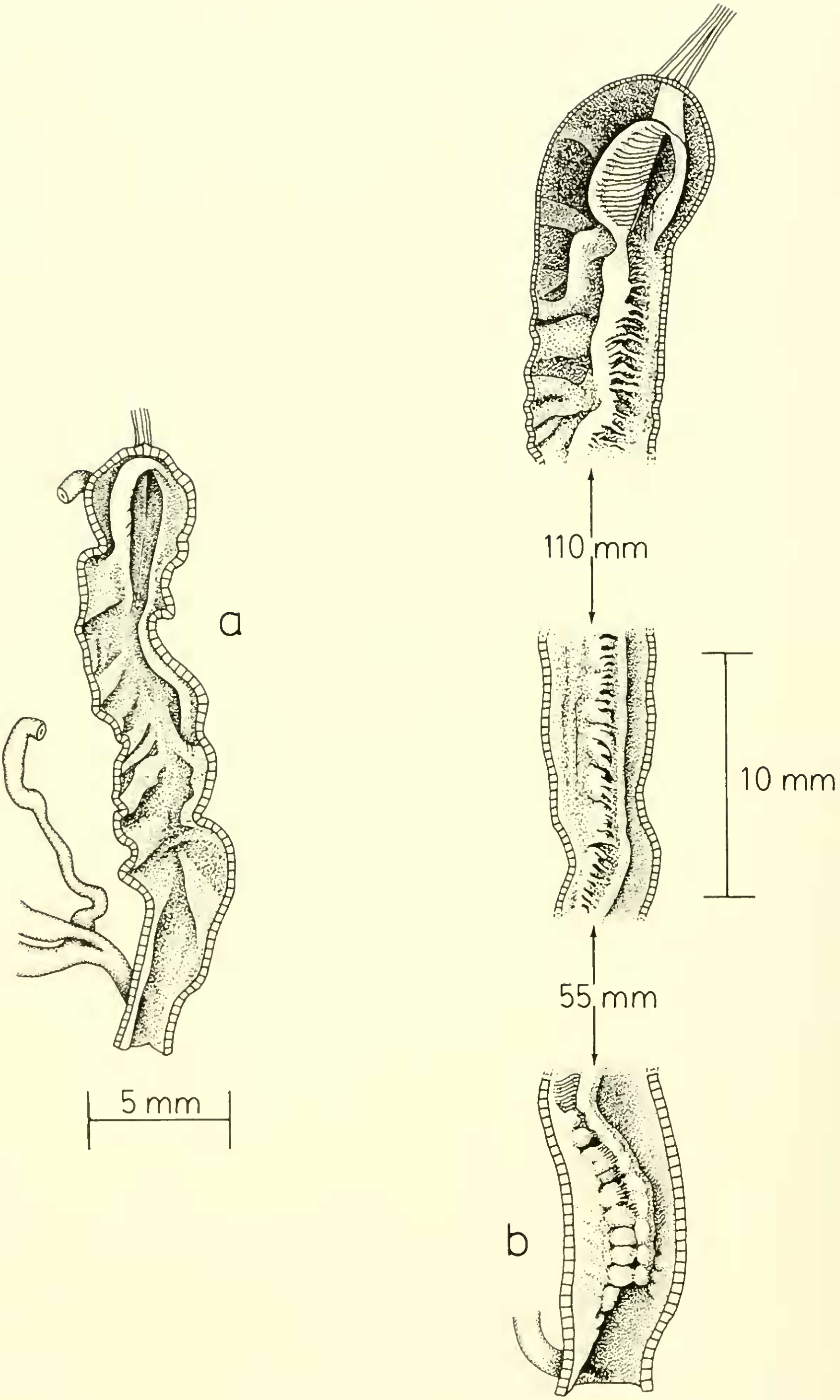


FIG. 18. Opened uneverted penial tubes. a. *Mesodon sayanus*, GS-130 #6: penial wall actually much thinner than shown here (also dissected #1, 4). b. *Mesodon chilhoweensis*, Hubricht 30943 #A (also dissected SC-263 #A: subadult with greatly flared chalice wall).

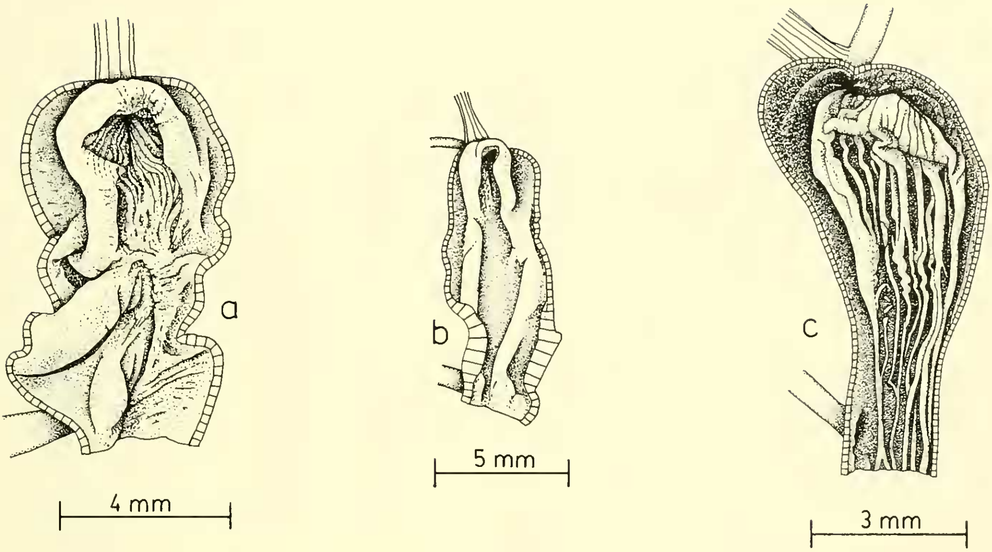


FIG. 19. Opened uneverted penial tubes. a. *Patera sargentiana,* GS-101 #1 (also dissected #9, 12). b. *Patera clarki,* GS-2 #5 (also dissected #6, 7; and other populations). c. *Patera appressa,* GS-104 #1 (also dissected #5, 7; GS-141 #2, 4, 6, 8). There is much variation in size of inflated chalice wall of *P. appressa;* illustrated specimen was opened from ventral side, such that opening of vas deferens appears to lie outside chalice.

right (ca. 0.3 mm), thence grading inconspicuously into right lateral pilaster. Penial wall otherwise free of structures (the transverse folds shown in Figure 18a are artifacts of preservation).

Mesodon (*Mesodon*) *clausus* (Say, 1821). (Fig. 16b) Dissections: seven from two populations. Length 9.8 mm, width 1.6 mm, curving strongly to left in upper third. Left lateral pilaster extending full length of penis, thick (0.4 mm), firm, cord-like. Right lateral pilaster extending entire length of penis, thick (0.3 to 0.4 mm), firm, and cord-like, except apically, where it is low and indistinct. Dorsal surface of penis covered with longitudinally parallel ridges, cord-like, ca. 0.2 mm wide basally, apically dividing to become narrower and less distinct, lateral-most ridges merging with apical right lateral pilaster or anastomosing with mid-region of left lateral pilaster. Ejaculatory pore seemingly flush with wall of penis. Right chalice wall 0.2 mm thick at edge, firm, flaring outward to form ear-like flap; right chalice wall thicker (0.3 mm), firm, cord-like basally, flaring outward apically to meet left chalice wall in apical point; chalice thus resembling pointed left ear, 1.7 mm long and 1.2 mm wide, pinna of which is rolled inward in uneverted, inactive state. Penial wall otherwise free of structures.

Mesodon (*Mesodon*) *sanus* (Clench & Archer, 1933). (Fig. 15a) Dissections: two from one population. Length 11.6 mm, width 2.2 mm. Left lateral pilaster seemingly extending full length of penis, firm, cord-like, 0.2 to 0.5 mm wide, seemingly merging baso-ventrally with right lateral pilaster. Right lateral pilaster extending whole length of penis, firm, cord-like, 0.2 mm wide. Entire dorsal surface of penis covered with field of closely-adjacent, longitudinally-arrayed, roughly parallel cord-like ridges, about 12 of them apically, averaging about 0.1 mm wide, but only about five of them basally and averaging ca. 0.2 mm wide by fusion with one another and with both lateral pilasters, with which they are intimately connected. Ejaculatory pore flush with wall of penis. Chalice a rounded ear-like flap, flared to left, about 0.1 mm thick at edge, and standing a maximum of about 1.1 mm high, rolled over toward right side in the uneverted penis. Penial wall without other sculptural features.

Mesodon (*Mesodon*) *thyroidus* (Say, 1817). (Fig. 15b) Dissections: nine from three populations. Length 12.5 mm, width 2.5 mm, gradually expanding apically, then constricting narrowly just below chalice to form shoulder, or shelf, before expanding again slightly to apex; penis thus of a three-dimensional shape diffi-

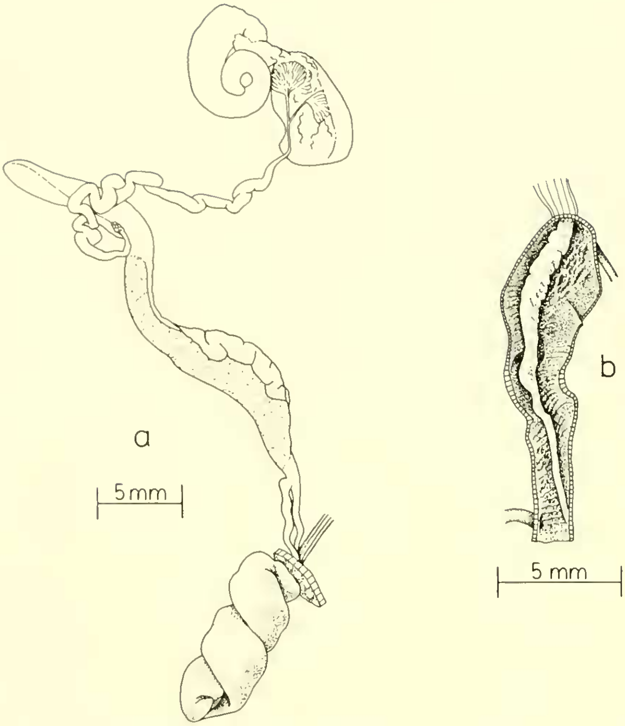


FIG. 20. Penial tubes of *Patera laevior*. a. H-22 #3: fully everted penis, and remaining internal reproductive system (compare with Figure 10). b. H-22 #A: opened uneverted penial tube [also dissected #1 (pilaster much more inflated and almost forming a chalice); GS-125 #1, 4, 5; and examined three everted penes from SC-217].

cult to pin out for clear viewing in two dimensions, hence the folds and distortions visible in Figure 15b. Left lateral pilaster extending full length of penis, firm, cord-like, ca. 0.5 mm wide throughout. Right lateral pilaster seemingly extending full length of penis, cord-like, apically separated from right chalice wall, expanding to width of approximately 0.8 mm in upper half of penis, then narrowing to about 0.4 mm in basal half, variable in width throughout. Dorsal wall of penis covered with field of somewhat parallel, somewhat longitudinally arranged cord-like ridges, ca. 0.3 mm wide, variously merging with one another and with both lateral pilasters (in Figure 15b several are merged to form the analog of a third pilaster beside the left lateral pilaster). Ejaculatory pore flush with wall of penis. Chalice in shape of left ear, rolled over to right in uneverted penis, 1.3 mm high at point. Penial wall seemingly free of other structures.

Mesodon (*Mesodon*) *trossulus* Hubricht, 1966. (Fig. 16c) Dissections: one from one population (topotype). Length 9.8 mm, width 1.4 mm, apex bent to left. Left lateral pilaster extending entire length of penis, its apex not continuous with left chalice wall, but to left of chalice, firm, cord-like, 0.3 mm wide apically, gradually tapering to ca. 0.1 mm basally. Right lateral pilaster firm, cord-like, 0.3 mm wide apically, tapering to 0.2 mm basally. Dorsal surface of penis covered with about 12 approximately parallel, thin (ca. 0.05 mm), cord-like ridges, variously branching and merging, most of them branching off at angle of about 15 degrees, step-like, from right lateral pilaster. Ejaculatory pore flush with wall of penis. Chalice shaped like left ear with apically pointed pinna, rolled to right in uneverted penis; unrolled length 2.0 mm, width 1.4 mm, edge thickness ca. 0.2 mm. Penial wall otherwise seemingly free of other structures (the wavering ventral gutter shown in Figure 16c is presumably an artifact).

Patera (*Patera*) *appressa* (Say, 1821). (Fig. 8c; opened ventrally, dorsal ridges central, lateral pilasters reversed as labeled) Dissections: seven from two populations. Length 7.2

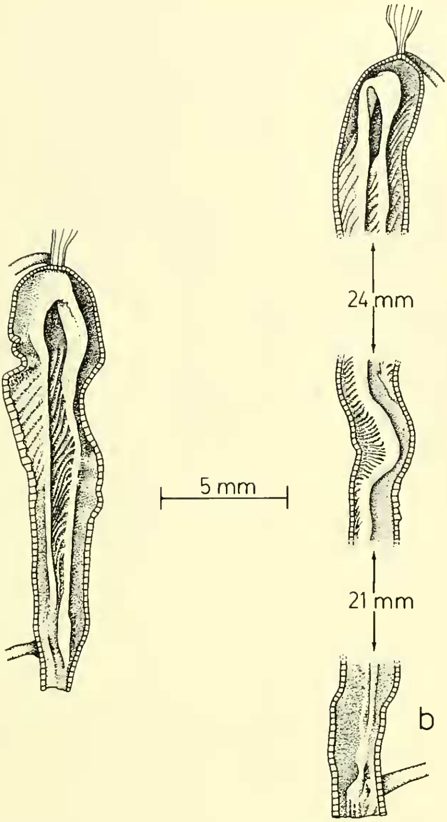


FIG. 21. Opened uneverted penial tubes. a. *Patera panselena,* GS-142 #9 (also dissected #2, 6). b. *Patera perigrapta,* GS-98 #8: whole length = 64 mm [also dissected #20, A, and examined #7, 9, and 18, each with partly everted penis (penis length varies greatly within this population); GS-3 #12; GS-57 #A; GS-90 #1; and examined one specimen with everted penis from each of the following populations: GS-170; SC-61; SC-65; SC-66; SC-67; SC-97].

mm, width 3.2 mm, apically expanded. Left lateral pilaster running entire length of penis, thin, cord-like, 0.2 mm wide at junction with left chalice wall, gradually tapering to minimal width of 0.1 mm at mid-penis. Right lateral pilaster running full length of penis, cord-like, uniformly wide in apical two-thirds (0.3 mm), whence tapering abruptly to 0.1 mm. Dorsal penial wall evenly covered with thin, cord-like, nearly parallel ridges, approximately alike in width, apically twice as wide (0.1 mm) as basally, variously branching and anastomosing with one another and with the lateral pilasters (Figure 19c shows a very close anastomosis between one of these ridges and the right lateral pilaster). Ejaculatory pore (shown above chalice in Figure 19c) flush with penial wall. Chalice (inverted in Figure 19c) with rather thin (0.3 mm), flexible walls, forming seemingly symmetrical, broad (3.0 mm) hood with estimated central depth of 0.7 mm. Penial walls otherwise free of scultpure.

Patera (*Patera*) *clarki* (Lea, 1858). (Fig. 19b) Dissections: three from one population. Length 9.1 mm, width 3.0 mm. Left lateral pilaster seemingly running entire length of penis, solid, thick, uniform in width (0.6 mm), abruptly but slightly tapering apically so as to become discrete from otherwise similar left wall of chalice. Right lateral pilaster running entire length of penis, solid, fairly uniform in width (0.6 mm), flattened in upper two-thirds so as to grade into penial wall, especially on dorsal side. Ejaculatory pore flush with penial wall. Chalice a symmetrical cowl, 2.7 mm long, 1.9 mm wide, distinct from lateral pilaster, its walls uniformly thick (0.3 mm). Penial walls free of sculpture.

Patera (*Patera*) *laevior* (Pilsbry, 1940). (Fig. 20) Dissections: nine from three populations (one population with penes already everted). Length 12.6 mm, width 2.0 mm. Left lateral pilaster extending entire length of penis, wavy or bulbous in outline, apically grading into left chalice wall, 0.8 mm wide in upper third, tapering gradually and irregularly to 0.3 mm in lower third. Right lateral pilaster absent or imperceptible. Ejaculatory pore flush with penial wall. Chalice inconspicuous, its left wall (0.5 mm wide) continuous with left lateral pilaster, and apically tapering rapidly to mere low arching ridge. Penial walls free of sculpture (the patterns of transverse folds and wavy, elongated pits shown in Figure 20b are interpreted as preservational artifacts).

Patera (*Patera*) *panselena* (Hubricht, 1976). (Fig. 21a) Dissections: three from one population. Length 15.1 mm, width 1.6 mm. Left and right lateral pilasters running full length of penis, equally narrow (0.2 mm) almost throughout, grading apically into chalice walls. Ejaculatory pore flush with penial wall. Chalice a shallow, thin-walled hood (0.8 mm deep, wall 0.3 mm thick), slightly asymmetric, extending 5.0 mm on right and 3.5 mm on left, tapering smoothly into lateral pilasters. Penial walls free of sculpture (all the diagonal folds shown in Figure 21a presumably are preservational artifacts).

Patera (*Patera*) *perigrapta* (Pilsbry, 1894b). (Fig. 21b) Dissections: 19 from ten popula-

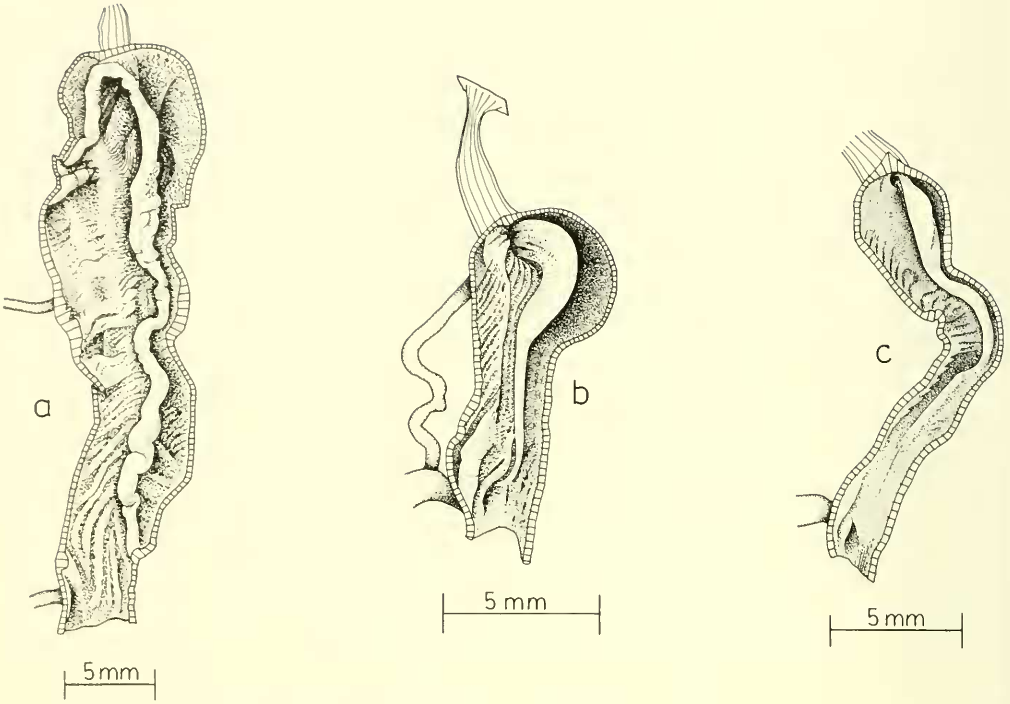


FIG. 22. Opened uneverted penial tubes. a. *Patera binneyana* "short", GS-95 #2 (also dissected Hubricht 31615 #A, B; Hubricht 33898 #A). b. *Patera leatherwoodi*, GS-67 #1 (also dissected GS-68 #1). c. *Patera roemeri*, GS-63 #21 (also dissected #4, 6, 7, 15).

tions (including 13 everted penes from seven populations). Length 65.4 mm (extremely variable in other examined specimens), width 1.8 mm. Left lateral pilaster extending entire length of penis, cord-like, fairly uniform in width (0.5 mm), gradually tapering basally (to 0.2 mm wide), apically grading into left wall of chalice. Right lateral pilaster extending along upper half of penis, where it is similar in width and appearance to left lateral pilaster. Ejaculatory pore flush with penial wall. Chalice a symmetric hood, 1.2 mm deep at apex, about 3.1 mm long, and with walls 0.2 mm thick that become lower basally to grade into lateral pilasters. Penial walls free of sculpture (the transverse grooves and diagonal folds shown in Figure 21b seem to be artifacts of preservation).

Patera (*Patera*) *sargentiana* (Johnson & Pilsbry, 1892). (Fig. 19a) Dissections: three from one population. Length 7.7 mm, width 2.9 mm. Left lateral pilaster seemingly running entire length of penis, solid, thick, broad (0.7 mm), seemingly discontinuous but uniform in width in lower half. Right lateral pilaster short (ca. 1.4 mm), flat, tapering rapidly from right chalice wall to merge with penial wall. Ejaculatory pore flush with penial wall. Chalice a thick-walled, symmetric hood (2.6 mm long, 3.1 mm wide, about 1.2 mm deep, walls 0.6 mm thick), its walls grading into lateral pilasters. Penial walls free of sculpture (Figure 19a shows both large- and small-scale structural artifacts due to severe contraction and folding of the specimen).

Patera (*Ragsdaleorbis*) *pennsylvanica* (Green, 1827). (Fig. 10b) Dissections: two from two populations. Length 13.8 mm, width 2.2 mm. Left lateral pilaster inconspicuous, extending about one-third of length of penis, 0.3 mm wide, not highly elevated above wall of penis. Right lateral pilaster extending to about mid-length of penis, like a thick (ca. 0.5 mm), high-standing (ca. 1.0 mm) ridge imperceptibly continuous with right chalice wall and basally tapering in height and, to lesser extent, in width. Ejaculatory pore on summit of somewhat barrel-shaped apical plug, or pedestal, 1.7 mm long, 1.7 mm wide at center. Chalice wall uniformly high (ca. 1.0 mm), about 0.2 mm

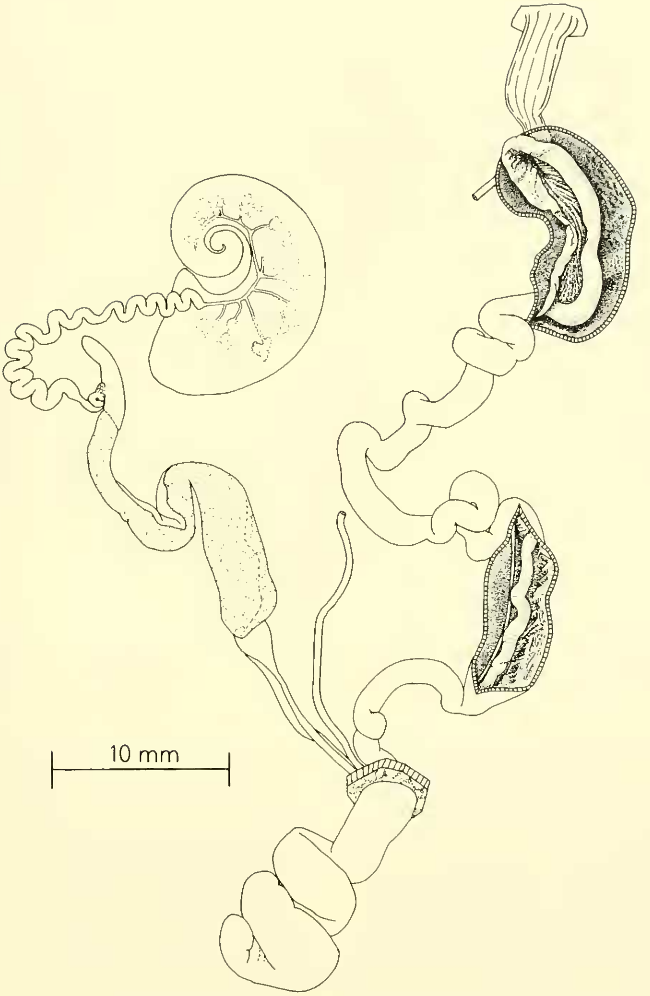


FIG. 23. Opened partly everted penial tube and remaining internal reproductive system of *Patera binneyana* "long", FMNH 176008 #C (also dissected #A, B; FMNH 176195 #A). Compare wtih Figure 12a.

thick at edge, well differentiated from left lateral pilaster to form flap on left, but undifferentiated from right lateral pilaster. Penial wall seemingly otherwise free of structures (the massive system of angular ridges shown in Figure 10b seems to consist of transient folds best considered preservational artifacts).

Patera (*Vesperpatera*) *binneyana* (Pilsbry, 1899). Two forms were found (see Appendix 1) and are described separately here.

P. binneyana "short." (Fig. 22a) Dissections: eight from eight populations. Length 30.6 mm, width 4.2 mm. Left lateral pilaster short, extending along only upper fifth to fourth of length of penis, 0.6 mm wide, cordlike at junction with left wall of chalice, flattening basally to merge gradually with penial wall. Right lateral pilaster extending entire length of penis, solid, lumpy, varying in width from 0.6 to 1.4 mm, wide at merger with right chalice wall. Ejaculatory pore flush with penial wall. Chalice an asymmetric hood (left side 4.3 mm long, right side 6.5 mm long), about 4.0 mm wide, 1.2 mm deep, its walls continuous with lateral pilasters and about 0.5 mm thick. Penial walls free of sculpture (patterns of folds shown in Figure 22a are preservational artifacts).

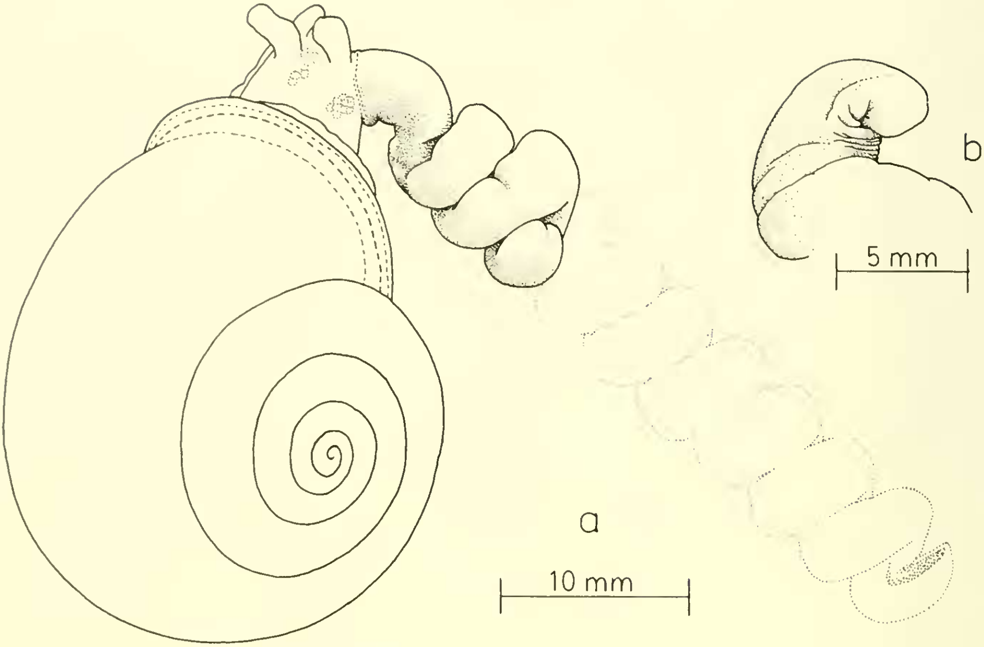


FIG. 24. Partly everted penial tube of *Patera binneyana* "long", FMNH 176008 #C. a. Actual and extrapolated everted penis (see Figure 10). b. Tip of actually everted penis showing lack of chalice or functional structure.

P. binneyana "long." (Figs. 23, 24) Dissections: four from two populations. Length 91.0 mm, width 2.7 mm. Left and right lateral pilasters seemingly extending along entire length of penis, left one very thin (0.1 mm) and cord-like, increasing in height (but not width) apically to juncture with left chalice wall. Right lateral pilaster thick and sausage-like throughout, 0.9 mm wide at mid-penis, 1.2 mm wide apically before constricting slightly at junction with right chalice wall. Ejaculatory pore flush with penial wall. Chalice a simple hood, its walls about 1.6 mm high and 0.5 mm thick, asymmetric, right side 7.1 mm long and left side 4.9 mm long. Penial walls free of sculpture (apical pits and mid-penial grooves shown in Figure 23 are considered preservational artifacts).

Patera (*Vesperpatera*) *clenchi* (Rehder, 1932). (Fig. 25a) Dissections: one from one population. Length 8.2 mm, width 1.1 mm. Left lateral pilaster obsolete, consisting of thickened region, 0.3 mm × 0.8 mm, at base of left chalice wall. Right lateral pilaster extending entire length of penis, solid, cord-like, 0.4 mm wide for most of length, tapering to 0.3 mm in upper fifth. Ejaculatory pore flush with penial wall. Chalice a simple hood, 1.1 mm wide, 1.1 mm long, its wall about 0.2 mm thick, right wall higher (0.3 mm) than left wall (0.2 mm). Penial walls free of sculpture (diagonal folds shown in Figure 25a seem to be due to contraction during preservation).

Patera (*Vesperpatera*) *indianorum* (Pilsbry, 1899). (Fig. 25b) Dissections: two from one population. Length 28.1 mm, width 2.8 mm. Left lateral pilaster seemingly extending full length of penis, flat, 0.9 mm wide, in some places difficult to distinguish from wall of penis, seemingly lessening considerably in width before joining left chalice wall. Right lateral pilaster extending along full length of penis, solid, cord-like, variable in width (0.4 to 1.3 mm), wide at junction with right chalice wall. Ejaculatory pore flush with penial wall. Chalice a simple hood, 4.9 mm wide, 4.9 mm long, its wall about 0.6 mm thick, right wall higher (1.5 mm) than left wall (1.1 mm). Penial walls free of sculpture (transverse folds shown in the lower half of Figure 25b are artifacts).

Patera (*Vesperpatera*) *kiowaensis* (Simpson, 1888). (Fig. 25c) Dissections: two from one population. Length 15.9 mm, width 1.4

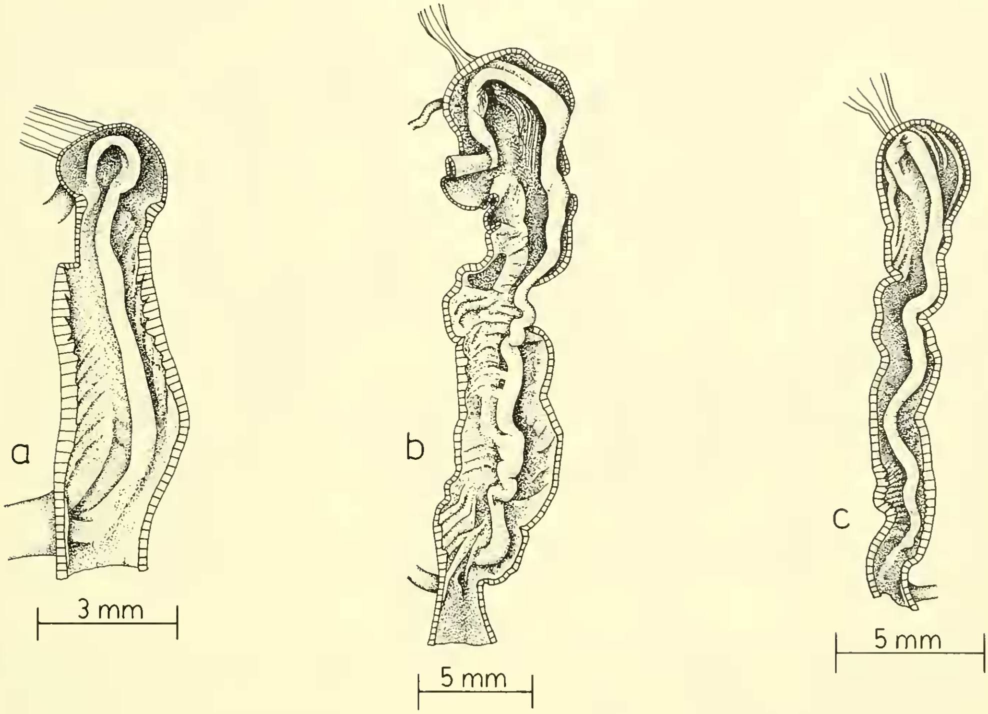


FIG. 25. Opened uneverted penial tubes. a. *Patera clenchi,* Hubricht 25210 #A. b. *Patera indianorum,* GS-87 #1 (also dissected #5). c. *Patera kiowaensis,* GS-84 #12 (also dissected #18).

mm. Left lateral pilaster seemingly absent, or at most a thickened streak at base of left chalice wall. Right lateral pilaster running full length of penis, solid, cord-like, variable in width (0.4 to 0.5 mm) for most of length, tapering basally to merge with wall of penis, apically grading imperceptibly into right chalice wall. Ejaculatory pore flush with penial wall. Chalice a simple hood, 1.4 mm wide, 2.0 mm long, wall about 0.3 mm thick, right wall higher (0.5 mm) than left wall (0.3 mm). Penial walls free of sculpture (apical longitudinal ridges and transverse basal folds shown in Figure 25c seem to be artifacts of preservation).

Patera (*Vesperpatera*) *leatherwoodi* (Pratt, 1971). (Fig. 22b) Dissections: two from two populations. Length 9.1 mm, width 1.4 mm, expanding apically to about 3.0 mm. Left lateral pilaster stretching about three-fourths of length of penis, very thin (0.1 mm) and inconspicuous. Right lateral pilaster reaching full length of penis, solid, cord-like, 0.3 mm wide at juncture with right chalice wall, gradually tapering basally to 1.0 mm wide. Ejaculatory pore flush with penial wall. Chalice like a spatula, right wall flared high (1.4 mm maximum), long (3.9 mm) and rounded; left wall lower (0.7 mm) and seemingly appressed to penial wall. Penial walls free of sculpture (the oblique folds and the large, short, basal thickening shown in Figure 22b are interpreted as preservational artifacts).

Patera (*Vesperpatera*) *roemeri* (Pfeiffer, 1848). (Fig. 22c) Dissections: five from one population. Length 16.6 mm, width 1.5 mm. Left lateral pilaster seemingly absent. Right lateral pilaster extending three-fourths of length of penis, solid, cord-like, and 0.4 mm wide below junction with right chalice wall, tapering and flattening in lower half to merge with penial wall. Ejaculatory pore flush with penial wall. Chalice like a spatula, right wall flared high (about 1.4 mm maximum), long (3.8 mm) and rounded; left wall vestigial or absent. Penial walls free of sculpture (left-hand, transverse grooves shown in Figure 22c are artifacts of preservation).

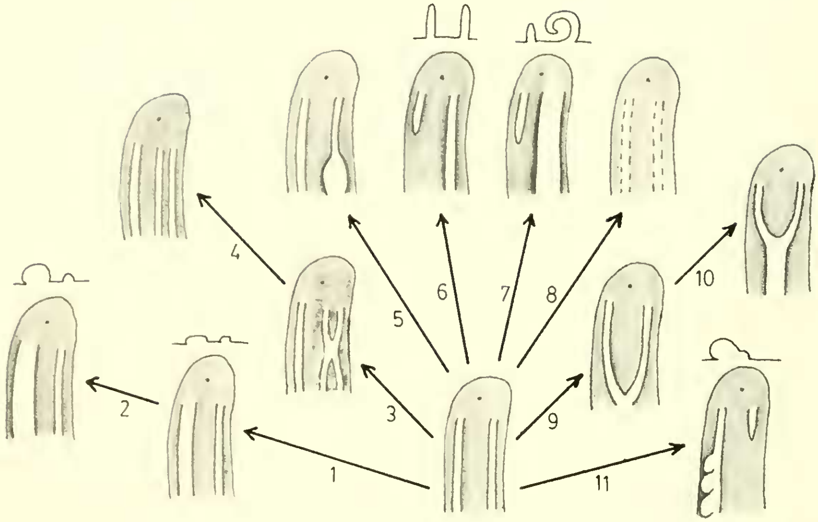


FIG. 26. Suggested character-state transformations in Mesodontini penial morphology: Character 1, lateral pilasters.

Suggested Character-State Transformations. The total variation in penial morphology was classified into five characters comprising 37 character states. These are arranged into their suggested phylogenies in Figures 26–28, in which the suggested character-state transformations are numbered 1–34.

The lateral pilasters (Character 1) vary greatly in the Mesodontini. Twelve states were detected, none of which seemed to be convergent. Their suggested phylogeny (Fig. 26) contains Transformations 1–11.

The shape of the chalice (Character 2) is the most variable feature of the mesodontin genitalia. Fourteen character states were detected, for which 14 transformations (Transformations 12–25) are suggested (Fig. 27). According to this hypothesis, there are three convergences: thick-walled, Λ-shaped chalices (Transformations 13 and 23); deep, cylindrical chalices (Transformations 16, 17–20, 25); and thin, high-standing chalice walls (Transformations 14, 22).

Character 3, baso-ventral structures, comprises three states, connected by suggested Transformations 26 and 27 (Fig. 28).

Dorsal structures (Character 4) yielded six character states, none of them detectably convergent (Fig. 28) and connected by six suggested transformations (Transformations 28–33). Other dorsal features, which are not included under this particular character, but which could have been, and which probably serve the same function, are the third pilaster (Fig. 13; Transformations 3, 4) and the basal bulges branching from the left pilaster (Fig. 11b, c; Transformation 11). Other dorsal sculptural features that appear in the illustrated dissections but were interpreted as preservational artifacts include the oblique folds in *Patera panselena* (Fig. 21a), *P. perigrapta* (Fig. 21b), *P. sargentiana* (Fig. 19a), *P. leatherwoodi* (Fig. 22b), *P. roemeri* (Fig. 22c), *P. laevior* (Fig. 20b), *P. clenchi* (Fig. 25a), *P. indianorum* (Fig. 25b), *P. kiowaensis* (Fig. 25c), *Mesodon sayanus* (Fig. 18a), *M. chilhoweensis* (Fig. 18b), *Inflectarius edentatus* (Fig. 12c), *I. inflectus* (Fig. 9a), *I. smithi* (Fig. 9c), *I. ferrissi* (Fig. 13c), *I. downieanus* (Fig. 10a), *Patera pennsylvanica* (Fig. 10b) and *P. kalmianus* (Fig. 11a); the irregular-network pattern in *Mesodon zaletus* (Fig. 4f), *Patera binneyana* (Fig. 23), *P. laevior* (Fig. 20b), *Inflectarius edentatus* (Fig. 12c), *Fumonelix jonesiana* (Fig. 8b) and *Inflectarius kalmianus* (Fig. 11a); the beaded and/or cuneiform sculpture next to a pilaster in *Mesodon chilhoweensis* (Fig. 18b) and *Inflectarius ferrissi* (Fig. 13c); and the transverse waves in *Mesodon normalis* (Fig. 11c).

The fifth and final character, peripheral structures, has only two states, connected by Transformation 34 (Fig. 28).

In presenting each of the 34 suggested character-state transformations below, the same format has been used throughout: (1)

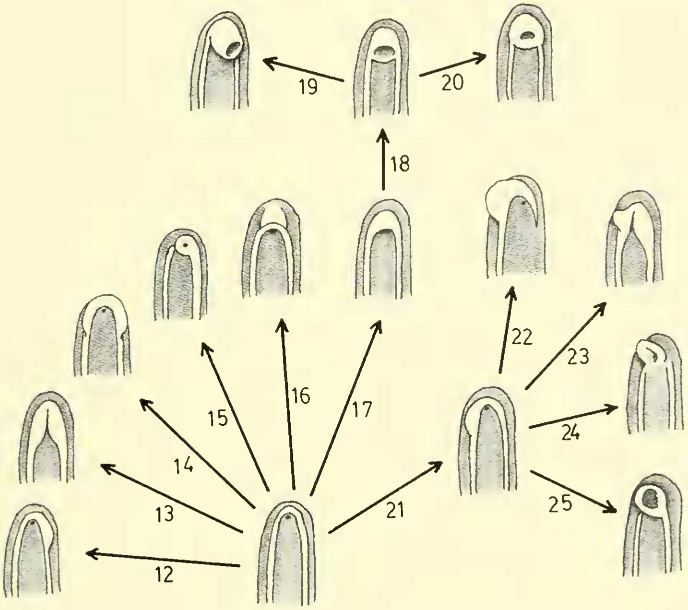


FIG. 27. Suggested character-state transformations in Mesodontini penial morphology: Character 2, chalice.

identification number as used in Figures 26–28; (2) number(s) of transformation(s) suggested to have preceded it in evolution; (3) suggested plesiomorphic state; (4) outgroup taxa having the suggested plesiomorphic state; (5) suggested apomorphic state; (6) taxa whose ancestor(s) are suggested to have had the apomorphic state, **although these taxa lack the state now;** (7) taxa that now have the suggested apomorphic state; and (8) discussion of the suggested transformation, including any further explanation, and the reasoning behind its suggestion. In defining the transformations, the terms distal and apical are used interchangeably, as are proximal and basal.

Transformation 1. Preceding transformations: none.

Plesiomorphic state: left pilaster distally higher than broad. Present in (outgroups): *Polygyra*, *Praticolella*, some *Stenotrema*, all Mesodontini except *I. inflectus*, *I. approximans*, *I. magazinensis* and *I. downieanus*.

Apomorphic state: left pilaster distally twice as broad as high, thick and fleshy. Formerly present in: *I. inflectus* (Fig. 9a), *I. approximans* (Fig. 12a), *I. magazinensis* (Fig. 12b), *I. downieanus* (Fig. 10a). Now present in: *I. inflectus* (Fig. 9a).

Discussion. The homology of the broad, thick left pilaster of these taxa is uncertain. The most problematic of these is that of *I. downieanus,* in which contractile distortion due to immersion of the specimen live in isopropynol renders interpretation difficult. The left pilaster of *I. inflectus* is attenuated, extending only half the length of the penis, whereas the left pilasters of *I. approximans* and *I. magazinensis* (and possibly *I. downieanus*) are full-length. These differences in degree of pilastral attenuation were not used for phylogenetic analysis because of possible intraspecific variation (compare Figs. 4h, 4i).

Transformation 2. Preceding transformations: 1.

Plesiomorphic state: left pilaster distally twice as broad as high, thick, fleshy; right pilaster pronounced. Present in (outgroup): *I. inflectus* (Fig. 19a).

Apomorphic state: left pilaster extremely thick and rounded, right pilaster obsolete to absent. Formerly and now present in: *I. approximans* (Fig. 12a), *I. magazinensis* (Fig. 12b), *I. downieanus* (Fig. 10a).

Discussion. As mentioned for Transformation 1, interpretation of *I. downieanus* is difficult and its homology for this character state is highly problematic, especially because its

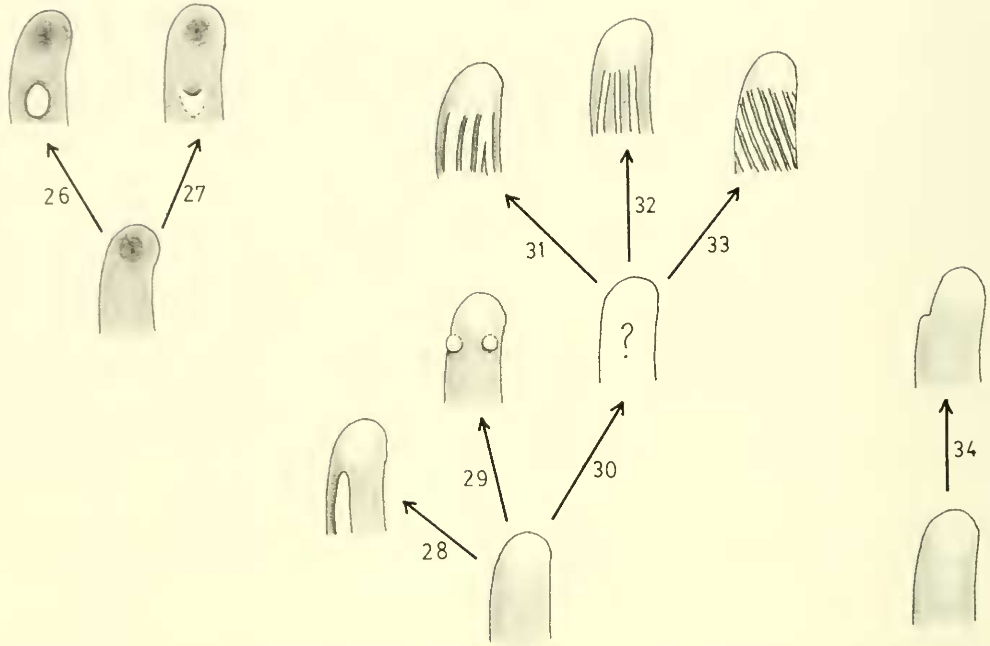


FIG. 28. Suggested character-state transformations in Mesodontini penial morphology: Characters 3, 4 and 5, baso-ventral structures, dorsal structures and peripheral structures.

right pilaster, although attenuated, is much more fully developed than in *I. approximans* and *I. magazinensis*. The latter two species, on the other hand, seem very similar and are much more likely to be homologous.

Transformation 3. Preceding transformations: none.

Plesiomorphic state: two lateral pilasters only. Present in (outgroups): *Polygyra, Praticolella,* most *Stenotrema,* all Mesodontini except *I. inflectus, I. rugeli, I. subpalliatus* and *I. ferrissi.*

Apomorphic state: third pilaster present and partly attached to right pilaster. Formerly present in: *I. subpalliatus* (Fig. 13a), *I. ferrissi* (Fig. 13c), *I. inflectus* (Fig. 19a), *I. rugeli* (Fig. 13b). Now present in *I. inflectus* (Fig. 9a).

Discussion. The longitudinally divided right pilaster of *I. inflectus* is unique. It is thought to represent an intermediate stage toward a complete longtiduinal division to produce a third pilaster (Transformation 4).

Transformation 4. Preceding transformations: 3.

Plesiomorphic state: third pilaster partly attached to right pilaster. Present in (outgroup): *I. inflectus* (Fig. 9a).

Apomorphic state: third pilaster separate from and parallel to right pilaster. Formerly and now present in: *I. subpalliatus* (Fig. 13a), *I. ferrissi* (Fig. 13c), *I. rugeli* (Fig. 13b).

Discussion. The structure here called a third pilaster is approximately equal in size, length and general appearance to the right and left lateral pilasters and is entirely parallel to them. It therefore seems not to be homologous with other dorsal structures such as long bulges (e.g. Fig. 8a), oblique branches from the pilasters (e.g. Fig. 7), and smaller and/or oblique basal ridges (e.g. Figs. 11b, 15c, 17b). Because it is near the right pilaster, the third pilaster is thought to be the result of longitudinal separation from the right pilaster, homologous to the condition in *I. inflectus.*

Transformation 5. Preceding transformations: none.

Plesiomorphic state: right pilaster basally unmodified. Present in (outgroups): *Polygyra, Praticolella, Stenotrema,* all Mesodontini except *I. smithi.*

Apomorphic state: right pilaster with basal swelling. Formerly and now present in: *I. smithi* (Fig. 9c).

Discussion. This character state seems not to be homologous with either basal bulges that are isolated from the right pilaster (Fig. 8), or basal enlargement due to merger of the right and left pilasters (Fig. 7).

Transformation 6. Preceding transformations: none.

Plesiomorphic state: neither lateral pilaster higher than four times its width. Present in (outgroups): *Polygyra, Praticolella, Stenotrema,* all Mesodontini except *P. pennsylvanica.*

Apomorphic state: both right and left pilasters about five times higher than wide, the right half-length and the left a short distal flap. Formerly and now present in: *P. pennsylvanica* (Fig. 10b).

Discussion. This unique character state is most similar to that of *F. wetherbyi* (Transformation 7), from which it differs in the equally high-standing pilasters and the flap-like end of the left pilaster.

Transformation 7. Preceding transformations: none.

Plesiomorphic state: Lateral pilasters no higher than five times their respective widths. Present in (outgroups): *Polygyra, Praticolella, Stenotrema,* all Mesodontini except *F. wetherbyi.*

Apomorphic state: right pilaster extremely high and thin (height more than six times width), full-length, and rolled over; left pilaster about three times higher than wide, and half-length. Formerly and now present in: *F. wetherbyi* (Fig. 9b).

Discussion. The unique right pilaster of *F. wetherbyi* is easily mistaken for a thick, broad pilaster whenever it is rolled over (Fig. 9b). Only when it is unrolled is its extreme height and thinness evident (see cross-section, Fig. 26). Its appearance in the everted penis is unknown, and its functional significance is unclear.

Transformation 8. Preceding transformations: none.

Plesiomorphic state: at least one lateral pilaster pronounced and conspicuous. Present in (outgroups): *Polygyra, Praticolella, Stenotrema,* all Mesodontini except *F. christyi, F. wheatleyi* and *F. jonesiana.*

Apomorphic state: both lateral pilasters greatly reduced to absent. Formerly and now present in: *F. christyi* (Fig. 8a), *F. wheatleyi* (Fig. 8c), *F. jonesiana* (Fig. 8b).

Discussion. This character state seems to be homologous in the three taxa, despite some differences in detail (Fig. 8). It is most clearly visible in *F. christyi,* in which the right and left pilasters are reduced to small but unmistakable traces, with the distal left pilaster the strongest remnant. In *F. wheatleyi,* this character state is complicated by the presence of seemingly inhomologous distal and basal bulges, but structures tentatively interpreted as remnant lateral pilasters occur as low ridges (Fig. 8c). In *F. jonesiana,* this character state is complicated by the presence of a long basal bulge, which might be a hypertrophied left pilaster, but which is interpreted here as a ventral basal bulge (Transformation 11), with the left pilaster fading proximally from a distally more pronounced region; the right pilaster appears fairly clearly as a slight trace (Fig. 8b).

Transformation 9. Preceding transformations: none.

Plesiomorphic state: lateral pilasters broadly separated basally. Present in (outgroups): *Polygyra, Praticolella,* some *Stenotrema,* all Mesodontini except *F. orestes* and *F. archeri.*

Apomorphic state: lateral pilasters meeting at their basal termini. Formerly present in: *F. orestes* (Fig. 8d), *F. archeri* (Fig. 7). Now present in: *F. orestes* (Fig. 8d).

Discussion. The right pilaster of *F. orestes* seems to be interrupted distally, whereas that of *F. archeri* is not; their basally-joining lateral pilasters might be independently derived, rather than homologous as here hypothesized.

Transformation 10. Preceding transformation: 9.

Plesiomorphic state: lateral pilasters meeting at their basal ends. Present in (outgroup): *F. orestes* (Fig. 8d).

Apomorphic state: lateral pilasters basally joined for about one-fourth their total lengths. Formerly and now present in: *F. archeri* (Fig. 7).

Discussion. See discussion under Transformation 9.

Transformation 11. Preceding transformations: none.

Plesiomorphic state: left pilaster basally a single ridge; right pilaster short to long.

Present in (outgroups): *Polygyra, Praticolella,* some *Stenotrema,* all Mesodontini except *M. normalis* and *M. andrewsae.*

Apomorphic state: left pilaster thick and dividing basally into network of bulges; right pilaster short. Formerly and now present in: *M. normalis* (Fig. 11c), *M. andrewsae* (Figs. 2, 11b).

Discussion. This clearly derived and presumably homologous character state differs in *M. andrewsae* and *M. normalis:* in the former the branching basal bulges are shorter and more pronounced. Because there is no basis for identifying one of these configurations as primitive, however, I have combined them as a single character state.

Transformation 12. Preceding transformations: none.

Plesiomorphic state: chalice walls undifferentiated from lateral pilasters. Present in (outgroups): *Polygyra, Praticolella,* some *Stenotrema,* and the mesodontins *P. panselena, P. perigrapta, P. sargentiana, P. clarki, P. appressa, P. binneyana, P. laevior, P. clenchi, P. indianorum, P. kiowaensis, I. approximans, I. magazinensis, I. edentatus, I. verus, I. inflectus, I. smithi* and *I. kalmianus* (Figs. 9a,c, 11a, 14, 18–25).

Apomorphic state: right chalice wall abruptly flared above right pilaster; left chalice wall and pilaster undifferentiated and greatly reduced. Formerly and now present in: *P. roemeri* (Fig. 22c), *P. leatherwoodi* (Fig. 22b).

Discussion. The flared right chalice wall is shown in side view in Figure 22b and in top view in Figure 22c. This change in elevation from the right pilaster is decidedly more abrupt than in *P. panselena* (Fig. 21a), *P. perigrapta* (Fig. 21b), *P. clarki* (Fig. 19b), or *P. clenchi* (Fig. 25), and these latter species also have more strongly developed left walls of the chalice, and thus their partial similarity is attributed to homoplasy or preservational artifact.

Transformation 13. Preceding transformations: none.

Plesiomorphic state: chalice walls not differentiated from lateral pilasters. Present in (outgroups): *Polygyra, Praticolella,* some *Stenotrema,* and the mesodontins *P. panselena, P. perigrapta, P. sargentiana, P. clarki, P. appressa, P. binneyana, P. laevior, P. clenchi, P. indianorum, P. kiowaensis, I. approximans, I. magazinensis, I. edentatus, I. verus, I. inflectus, I. smithi* and *I. kalmianus* (Figs. 9a,c, 11a, 14, 18–25).

Apomorphic state: right and left chalice walls thick and evenly rounded, enlarging smoothly from the lateral pilasters, and forming a Λ-shaped cleft. Formerly and now present in: *M. elevatus* (Figs. 4f–j, 6d–f).

Discussion. As discussed previously, the two dissected populations of *M. elevatus* differ considerably in their manifestation of this character state. The similarity in shapes of chalices of *M. elevatus* and the occasionally sympatric *M. zaletus* (Transformation 23) is attributed to homoplasy owing to the differences in structural detail previously discussed.

Transformation 14. Preceding transformations: none.

Plesiomorphic state: chalice walls not differentiated from lateral pilasters. Present in (outgroups): *Polygyra, Praticolella,* some *Stenotrema,* and the mesodontins *P. panselena, P. perigrapta, P. sargentiana, P. clarki, P. appressa, P. binneyana, P. laevior, P. clenchi, P. indianorum, P. kiowaensis, I. approximans, I. magazinensis, I. edentatus, I. verus, I. inflectus, I. smithi* and *I. kalmianus* (Figs. 9a,c, 11a, 14, 18–25).

Apomorphic state: chalice walls abruptly higher-standing than lateral pilasters, thin and symmetric or expanding slightly to right. Formerly and now present in: *I. subpalliatus* (Fig. 13a), *I rugeli* (Fig. 13b).

Discussion. This thin, high-standing chalice wall differs from that in *M. andrewsae, M. normalis* and *M. altivagus* (Transformation 22) in being symmetric or flared to the right rather than strongly flared to the left.

Transformation 15. Preceding transformations: none.

Plesiomorphic state: chalice walls not differentiated from lateral pilasters. Present in (outgroups): *Polygyra, Praticolella,* some *Stenotrema,* and the mesodontins *P. panselena, P. perigrapta, P. sargentiana, P. clarki, P. appressa, P. binneyana, P. laevior, P. clenchi, P. indianorum, P. kiowaensis, I. approximans, I. magazinensis, I. edentatus, I. verus, I. inflectus, I. smithi* and *I. kalmianus* (Figs. 9a,c, 11a, 14, 18–25).

Apomorphic state: chalice resembling thick wooden spoon, with right pilaster as its handle. Formerly and now present in: *I. ferrissi* (Fig. 13c).

Discussion. This type of chalice is both unique and very aberrant, without plausible connection with any other existing type.

Transformation 16. Preceding transformations: none.

Plesiomorphic state: chalice walls not differentiated from lateral pilasters. Present in (outgroups): *Polygyra, Praticolella,* some *Stenotrema,* and the mesodontins *P. panselena, P. perigrapta, P. sargentiana, P. clarki, P. appressa, P. binneyana, P. laevior, P. clenchi, P. indianorum, P. kiowaensis, I. approximans, I. magazinensis, I. edentatus, I. verus, I. inflectus, I. smithi* and *I. kalmianus* (Figs. 9a,c, 11a, 14, 18–25).

Apomorphic state: chalice floor deeply recessed to form symmetric, cylindrical pit skirted by undifferentiated chalice walls. Formerly and now present in: *P. pennsylvanica* (Fig. 10b).

Discussion. Despite a superficial resemblance to the deep chalices of *F. christyi, F. jonesiana, F. wheatleyi, F. orestes, F. archeri* and *M. mitchellianus* (Transformations 17–20, 25), the chalice of *P. pennsylvanica* is almost certainly inhomologous owing to its unique relationship to the normal chalice walls, which are continuous with and undifferentiated from the lateral pilasters.

Transformation 17. Preceding transformations: none.

Plesiomorphic state: chalice walls not differentiated from lateral pilasters. Present in (outgroups): *Polygyra, Praticolella,* some *Stenotrema,* and the mesodontins *P. panselena, P. perigrapta, P. sargentiana, P. clarki, P. appressa, P. binneyana, P. laevior, P. clenchi, P. indianorum, P. kiowaensis, I. approximans, I. magazinensis, I. edentatus, I. verus, I. inflectus, I. smithi* and *I. kalmianus* (Figs. 9a,c, 11a, 14, 18–25).

Apomorphic state: apical chalice wall forming symmetrical hood with moderately thick rim. Formerly present in: *F. christyi* (Fig. 8a), *F. wheatleyi* (Fig. 8c), *F. jonesiana* (Fig. 8b), *F. orestes* (Fig. 8d), *F. wetherbyi* (Fig. 9b). Now present in: *F. christyi* (Fig. 8a).

Discussion. Despite a superficial resemblance to the symmetrical, cylindrical chalice of *P. pennsylvanica* (Transformation 16), difference in structural detail suggests that this type of chalice arose by modification of the primitive walls of the chalice rather than by sinking of its floor.

Transformation 18. Preceding transformation: 17.

Plesiomorphic state: floor of hooded chalice continuous with ventral penial wall; chalice walls straight-sided. Present in (outgroup): *F. christyi* (Fig. 8a).

Apomorphic state: floor of hooded chalice separated from ventral penial wall by a continuous, moderately thick circular rim around chalice; chalice walls straight-sided to weakly convex. Formerly present in: *F. wheatlyi* (Fig. 8c), *F. jonesiana* (Fig. 8b), *F. orestes* (Fig. 8d), *F. archeri* (Fig. 7), *F. wetherbyi* (Fig. 9b). Now present in: none.

Discussion. It is most parsimonious, and seems developmentally most likely, that all symmetrical, circular-rimmed cup-like or cylindrical chalices formed by development of their walls as both homologous and derived from the simple hooded chalice of *F. christyi* (Fig. 8a) by way of this hypothetically intermediate stage. The ventral part of the continuous rim seems weak in *F. jonesiana* and *F. archeri,* stronger in *F. wheatleyi,* and very strong in *F. orestes;* these differences have been pooled because of possible individual variation. The ventral rim in *F. wetherbyi* is extreme.

Transformation 19. Preceding transformations: 17, 18.

Plesiomorphic state: circular rim of chalice rather thick; walls of chalice straight-sided to weakly convex. Present in (outgroup): hypothetical ancestor.

Apomorphic state: circular rim of chalice thin; chalice walls thin, very high-standing, and straight-sided to weakly convex. Formerly and now present in: *F. wetherbyi* (Fig. 9b).

Discussion. This highly derived type of chalice is difficult to illustrate (Fig. 26), and the representation of it in Figure 9b is misleading owing to initial misinterpretation of its structure. In this figure, the high, thin walls are folded down into the mouth of the chalice, making the chalice seem shorter, thicker, and smaller-mouthed than it really is; in its naturally extended state, the chalice probably resembles a tall, symmetric cylinder. As discussed previously, its affinities are problematic, but seem closest to the type of *F. wheatleyi* (Figs. 7, 8b–d), hence the hypothesized homology. It differs from the homoplasic chalice of *M. mitchellianus* (Transformation 25) in its symmetry and smooth, unserrated rim.

Transformation 20. Preceding transformations: 17, 18.

Plesiomorphic state: circular rim of chalice rather thick; chalice walls straight-sided to weakly convex. Present in (outgroup): hypothetical ancestor.

Apomorphic state: circular rim of chalice very thick; chalice walls convexly rounded. Formerly and now present in: *F. wheatleyi* (Fig. 8c), *F. jonesiana* (Fig. 8b), *F. orestes* (Fig. 8d, *F. archeri* (Fig. 7).

Discussion. This character state often resembles a recumbent, thick-walled Chinese teacup, best seen in the illustration of *F. wheatleyi* (Fig. 8c). As mentioned in the discussion of the preceding Transformation, the differences in this type of chalice among the four species having it have not been scored separately, because the relationship of these interspecific differences to individual variation is uncertain.

Transformation 21. Preceding transformations: none.

Plesiomorphic state: chalice walls not differentiated from lateral pilasters. Present in (outgroups): *Polygyra, Praticolella*, some *Stenotrema*, and the mesodontins *P. panselena, P. perigrapta, P. sargentiana, P. clarki, P. appressa, P. binneyana, P. laevior, P. clenchi, P. indianorum, P. kiowaensis, I. approximans, I. magazinensis, I. edentatus, I. verus, I. inflectus, I. smithi* and *I. kalmianus* (Figs. 9a,c, 11a, 14, 18–25).

Apomorphic state: left wall of chalice moderately flared. Formerly present in: *M. sayanus* (Fig. 18a), *M. chilhoweensis* (Fig. 18b), *M. normalis* (Fig. 11c), *M. altivagus* (Fig. 15c), *M. andrewsae* (Figs. 2, 11b), *M. zaletus* (Figs. 4a–e, 6a–c, 16), *M. mitchellianus* (Fig. 16a), *M. clausus* (Fig. 16b), *M. trossulus* (Fig. 16c), *M. thyroidus* (Fig. 15b), *M. sanus* (Fig. 15a), *I. downieanus*? (Fig. 10a). Now present in: *M. sayanus* (Fig. 18a), *M. chilhoweensis* (Fig. 18b).

Discussion. The chalices of all these taxa are flared to the left, usually with a left-hand flap. It is hypothesized, therefore, that they are homologous and derived from a common ancestor with the sort of moderate left-hand flare that occurs in *M. sayanus* and is more developed in *M. chilhoweensis*.

Transformation 22. Preceding transformation: 21.

Plesiomorphic state: left wall of chalice rather flared. Present in (outgroup): *M. sayanus* (Fig. 18a), *M. chilhoweensis* (Fig. 18b).

Apomorphic state: chalice asymmetrically scoop-shaped, left wall flared, high-standing, and thin-walled. Formerly and now present in: *M. normalis* (Fig. 11c), *M. altivagus* (Fig. 15c), *M. andrewsae* (Figs. 2, 11b).

Discussion. This kind of chalice differs from that of *I. subpalliatus* and *I. rugeli* (Transformation 14), which it superficially resembles in its strong left-hand asymmetry, whereas the other is symmetrical or flared to the right. The chalice of the illustrated specimen of *M. altivagus* (Fig. 15c) has a puckered rim; relaxed, undistorted examples resemble those of *M. andrewsae* and *M. normalis* in shape. This character state seems to be derivable from the kind occurring in *M. chilhoweensis* (Fig. 18b) by uniformly greater growth of the chalice walls.

Transformation 23. Preceding transformation: 21.

Plesiomorphic state: left wall of chalice rather flared. Present in (outgroup): *M. sayanus* (Fig. 18a), *M. chilhoweensis* (Fig. 18b).

Apomorphic state: right and left walls of chalice thick and rounded; enlarging rapidly from lateral pilasters, the right larger than the left, the left bearing a flap; and forming a Λ-shaped cleft. Formerly and now present in *M. zaletus* (Figs. 4a–e, 6a–c, 17).

Discussion. This unique sort of chalice seems to be convergent with that of *M. elevatus* (Figs. 4f–j, 6d–f); see discussion under Transformation 13. Its left-hand flap suggests a possible derivation from the sort in *M. chilhoweensis* (Fig. 18b) by thickening of both walls and restriction of the left-hand flare.

Transformation 24. Preceding transformation: 21.

Plesiomorphic state: left wall of chalice rather flared. Present in (outgroup): *M. sayanus* (Fig. 18a), *M. chilhoweensis* (Fig. 18b).

Apomorphic state: chalice narrowly triangular, inclined to the left, rolled over, thick-edged, with pore on right side. Formerly and now present in: *M. clausus* (Fig. 16b), *M. trossulus* (Fig. 16c), *M. thyroidus* (Fig. 15b), *M. sanus* (Fig. 15a).

Discussion. This sort of chalice is very distinctive and is almost certainly homologous in the four taxa. It conceivably could have derived from the kind in *M. normalis* (Transformation 22), rather than directly from that in *M. chilhoweensis* (Transformation 21) as hypothesized here.

Transformation 25. Preceding transformation: 21.

Plesiomorphic state: left wall of chalice rather flared. Present in (outgroup): *M. sayanus* (Fig. 18a), *M. chilhoweensis* (Fig. 18b).

Apomorphic state: chalice an asymmetric cylinder, taller on left side; wall and rim of chalice thin, the right rim serrated. Formerly and now present in: *M. mitchellianus* (Fig. 16a).

Discussion. Affinities of this unique kind of chalice are problematic. Despite a superficial resemblance to the deep chalices represented by Transformations 17–20 and 16, it differs in its asymmetry, its serrated right rim, and its continuity with the right pilaster but not the left pilaster (in which it is reminiscent of that in *M. ferrissi*, Fig. 13c). Its taller left wall suggests derivation from a homologue of the sort in *M. chilhoweensis* by way of unknown intermediates.

Transformation 26. Preceding transformations: none.

Plesiomorphic state: ventral penial wall smooth and featureless. Present in (outgroups): some *Polygyra*, some *Praticolella*, some *Stenotrema*, all Mesodontini except *F. wheatleyi, F. jonesiana, F. orestes, F. archeri.*

Apomorphic state: ventral penial wall bearing thick basal bulge. Formerly and now present in: *F. wheatleyi* (Fig. 8c), *F. jonesiana* (Fig. 8b), *F. orestes* (Fig. 8d), *F. archeri* (Fig. 7).

Discussion. This baso-ventral bulge varies somewhat in size, shape and position among *F. wheatleyi, F. orestes* and *F. archeri*, but it is assumed to be homologous. In *F. jonesiana* it is displaced to the left and is very large and elongate; thus it might not be homologous with that of the other three species. It does seem to be homologous with the bulge in *F. wheatleyi*, however. Even if the mid-ventral and left-ventral bulges are inhomologous, that of *F. jonesiana* still falls within the range of variation evident in *F. wheatleyi.*

Transformation 27. Preceding transformations: none.

Plesiomorphic state: ventral penial wall smooth and featureless. Present in (outgroups): some *Polygyra*, some *Praticolella*, some *Stenotrema*, all Mesodontini except *F. wheatleyi, F. jonesiana, F. orestes, F. archeri.*

Apomorphic state: ventral penial wall bearing basal pocket that opens toward apex. Formerly and now present in: *M. mitchellianus* (Fig. 16a).

Discussion. This basal pocket, shown in Figure 16a as a notch to the left of and slightly above the vaginal opening, is formed by a fold looping between the bases of the right and left lateral pilasters. This fold seems independent of the pilasters themselves, and therefore is not homologous with the basally joined pilasters of *F. orestes* (Fig. 8d) and *F. archeri* (Fig. 7), despite a superficial resemblance. This pocket, or pouch, occurred in all six dissected specimens (from two populations) of *M. mitchellianus;* it certainly is not an artifact of preservation.

Transformation 28. Preceding transformations: none.

Plesiomorphic state: dorsal wall of penis smooth and featureless. Present in (outgroups): many *Polygyra*, many *Praticolella*, some *Stenotrema*, and the mesodontins *P. panselena, P. perigrapta, P. sargentiana, P. clarki, P. binneyana, P. leatherwoodi, P. roemeri, P. laevior, P. clenchi, P. indianorum, P. kiowaensis, I. magazinensis, I. edentatus, I. verus, I. inflectus, F. wetherbyi, I. smithi, I. subpalliatus, I. rugeli, I. ferrissi, I. downieanus, P. pennsylvanica, F. jonesiana, F. orestes, F. archeri, I. kalmianus* and *M. normalis* (Figs. 7, 8b,d, 9, 10, 11a,b, 12–14, 18, 19a,b, 20–25).

Apomorphic state: dorsal wall of penis with elongate bulge on left side. Formerly and now present in: *F. christyi* (Fig. 8a), some specimens of *F. wheatleyi.*

Discussion. This dorsal bulge parallels the left lateral pilaster and might join it basally. In this respect it is homoplasic with the third pilaster (Transformation 4), from which it differs in being much thicker and more rounded, and is therefore more like the baso-ventral bulge (Transformation 26).

Transformation 29. Preceding transformations: none.

Plesiomorphic state: dorsal wall of penis smooth and featureless. Present in (outgroups): many *Polygyra*, many *Praticolella*, some *Stenotrema*, and the mesodontins *P. panselena, P. perigrapta, P. sargentiana, P. clarki, P. binneyana, P. leatherwoodi, P. roemeri, P. laevior, P. clenchi, P. indianorum, P. kiowaensis, I. magazinensis, I. edentatus, I. verus, I. inflectus, F. wetherbyi, I. smithi, I. subpalliatus, I. rugeli, I. ferrissi, I. downieanus, P. pennsylvanica, F. jonesiana, F. orestes, F. archeri, I. kalmianus* and *M. normalis* (Figs. 7, 8b,d, 9, 10, 11a,b, 12–14, 18, 19a,b, 20–25).

Apomorphic state: dorsal wall of penis bearing isolated apico-lateral bulges, one on each side. Formerly and now present in: some specimens of *F. wheatleyi* (Fig. 8c).

Discussion. This unique character state is clearly derived. It seems not to be associated with the lateral pilasters.

Transformation 30. Preceding transformations: none.

Plesiomorphic state: dorsal wall of penis smooth and featureless. Present in (outgroups): many *Polygyra*, many *Praticolella*, some *Stenotrema*, and the mesodontins *P. panselena, P. perigrapta, P. sargentiana, P. clarki, P. binneyana, P. leatherwoodi, P. roemeri, P. laevior, P. clenchi, P. indianorum, P. kiowaensis, I. magazinensis, I. edentatus, I. verus, I. inflectus, F. wetherbyi, I. smithi, I. subpalliatus, I. rugeli, I. ferrissi, I. downieanus, P. pennsylvanica, F. jonesiana, F. orestes, F. archeri, I. kalmianus* and *M. normalis* (Figs. 7, 8b,d, 9, 10, 11a,b, 12–14, 18, 19a,b, 20–25).

Apomorphic state: dorsal wall of penis bearing multiple, semi-parallel ridges. Formerly present in: *P. appressa* (Fig. 19c), *M. zaletus* (Figs. 4a–e, 6a–c, 17), *M. elevatus* (Figs. 4f–j, 6d–f), *M. andrewsae* (Figs. 2, 11b), *M. mitchellianus* (Fig. 16a), *M. clausus* (Fig. 16b), *M. trossulus* (Fig. 16c), *M. sanus* (Fig. 15a), *M. thyroidus* (Fig. 15b), *M. altivagus* (Fig. 15c). Now present in: none.

Discussion. Because there is considerable and incompletely understood variation within each of the three types of dorsal ridges here tentatively recognized (Fig. 28; Transformations 31–33), it is hypothesized that all three evolved from a common ancestral type of unknown appearance. More careful investigation of the dorsal ridges, including studies of ontogenetic and individual variation, should be very valuable and might well alter this suggestion of general homology.

Transformation 31. Preceding transformation: 30.

Plesiomorphic state: dorsal wall of penis bearing several semi-parallel ridges. Present in (outgroup): hypothetical ancestor.

Apomorphic state: dorsal ridges thick, irregular in width, and semi-parallel. Formerly and now present in: *M. andrewsae* (Figs. 2, 11b).

Discussion. These dorsal ridges are usually more than 0.5 mm wide and longitudinal. Perhaps they evolved from thin dorsal ridges (Transformation 32), or vice versa; as a compromise it is suggested that Transformations 31 and 32 arose independently from a common ancestor.

Transformation 32. Preceding transformation: 30.

Plesiomorphic state: dorsal wall of penis bearing multiple, semi-parallel ridges. Present in (outgroup): hypothetical ancestor.

Apomorphic state: dorsal ridges thin, irregular in width, and semi-parallel. Formerly and now present in: *P. appressa* (Fig. 19c), *M. zaletus* (Figs. 4a–e, 6a–c, 11), *M. elevatus* (Figs. 4f–j, 6d–f), *M. mitchellianus* (Fig. 16a).

Discussion. These dorsal ridges are usually less than 0.25 mm wide and longitudinal, but they can be slightly oblique (e.g. Figs. 4c, 6b, 16a). Whether the dorsal ridges in all four species are homologous is very problematic; because the variation is so great, and occasionally overlapping, in both *M. zaletus* and *M. elevatus* (Figs. 4, 6), and because their collective variation seems to overlap the conditions in both *P. appressa* and *M. mitchellianus*, homology is hypothesized.

Transformation 33. Preceding transformation: 30.

Plesiomorphic state: dorsal wall of penis bearing several semi-parallel ridges. Present in (outgroup): hypothetical ancestor.

Apomorphic state: dorsal ridges thin to thick, uniform in width, and parallel. Formerly and now present in: *M. clausus* (Fig. 16b), *M. trossulus* (Fig. 16c), *M. sanus* (Fig. 15a), *M. thyroidus* (Fig. 15b), *M. altivagus* (Fig. 15c).

Discussion. These dorsal ridges are usually 0.25–0.5 mm wide (but ca. 1 mm in *M. altivagus*) and usually oblique. They are much more even and corrugated than the other two kinds of dorsal ridges (Transformations 31, 32). The dorsal ridges of *M. altivagus*, although similar in general appearance, are proportionately larger than those of the other species, and might not be homologous.

Transformation 34. Preceding transformations: none.

Plesiomorphic state: both peripheries of penis smoothly straight or curving. Present in (outgroups): *Polygyra, Praticolella, Stenotrema*, all Mesodontini except *M. thyroidus*.

Apomorphic state: right periphery of penis abruptly stepped near apex to form shoulder. Formerly and now present in: *M. thyroidus* (Fig. 15b).

Discussion. Only in the naturally everted

TABLE 1. Distribution of 34 suggested genitalic character-state transformations (Figs. 26–28) among 42 species of Mesodontini. For correct gender endings of species, see Table 6 and text, excluding Appendix 3.

	Transformation Number																																	
Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34
OUTGROUPS	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
perigraptus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
panselenus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
sargentianus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
laevior	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
clarki	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
binneyanus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
indianorum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
clenchi	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
kiowaensis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
edentatus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
verus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
kalmianus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
approximans	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
magazinensis	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
downieanus	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
inflectus	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
rugeli	0	0	1	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
subpalliatus	0	0	1	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
ferrissi	0	0	1	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
smithi	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
pennsylvanicus	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
wetherbyi	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
christyi	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
wheatleyi	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	1	0	1	0	0	0	0	0	1	0	1	1	0	0	0	0	0
jonesianus	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	1	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0
archeri	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	1	1	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0
orestes	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	1	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0
normalis	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0
andrewsae	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	1	1	0	0	0
roemeri	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
leatherwoodi	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
elevatus	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0
sayanus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
chilhoweensis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
zaletus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	1	0	1	0	0
mitchellianus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	1	0	0	1	0	1	0	0
clausus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	1	0	0	1	0
trossulus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	1	0	0	1	0
sanus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	1	0	0	1	0
thyroidus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	1	0	0	1	1
altivagus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	1	0	0	1	0
appressus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0

penis is this penial shoulder obvious (Webb 1954b: figs. 3, 4). In the opened, uneverted penis (Fig. 15b), the shoulder appears as a kink in the wall that easily might be mistaken for a preservational artifact were it not for its consistent presence in all dissections.

Presence or absence of each of these 34 suggested anatomical transformations in each species of the Mesodontini is presented in Table 1.

Allozymic Analysis

Table 2 summarizes the complete electrophoretic results. In this table, each allele (electromorph) is represented by its migration distance relative to the control, *Mesodon zaletus* from Monte Sano, Alabama (FMNH 214772, 214773), the migration distance of which was arbitrarily set at 100 mm. For the 75 populations presented in Table 2, 95

TABLE 2. Allozyme data for 81 populations comprising 39 species of Mesodontini, and one population of the outgroup *Ashmunella*. Alleles for each of 16 loci are identified by their distances on the gels in mm relative to the most common allele of the control population (*Mesodon zaletus*, FMNH 214891), arbitrarily assigned a distance of 100 mm. Generic assignments (*M.* = *Mesodon*) are those of Pilsbry (1940); for revised generic assignments see Table 6.

Species	FMNH Catalogue Number	N	Sordh	Mdh-1	Mdh-2	Me	Icd	Pgd	Gd-1	Gd-2	Sod-1	Sod-2	Got-1	Got-2	Pgm	Lap	Mpi	Gpi
M. altivagus	214614	19	100	100	100	100	100	100	100	100	100	100	100	97	103(.42) 100(.58)	96	100	100
M. andrewsae	214618	13	100	100	100	100	103	100	101	99	100	110	103(.04) 100(.96)	97	103	104(.58) 102(.31) 96(.11)	96	105(.15) 100(.85)
M. appressus	214686	13	102	100	100	100	103	100	103	98	100(.08) 90(.92)	100	100	97	97(.58) 95(.15) 91(.27)	98(.54) 95(.46)	100	100(.12) 95(.88)
M. approximans	214623	1	100	99	100	100	103	100	103	99	100	100	97	97	105	98	96	100
M. binneyanus	214625	5	100	96	100	100	103	100	103	99	100	107	100	97	99(.70) 95(.30)	97	100	100
M. chilhoweensis	214627	15	100	100	100	104(.07) 101(.93)	103	100	102	100	100	100	103	97	100(.47) 98(.47) 95(.06)	97	100(.03) 96(.97)	105(.07) 100(.90) 95(.03)
M. christyi	214631	9	103	100	100	100	97	100	102	100	100	100	101	97	99(.78) 97(.05) 95(.17)	99(.94) 97(.06)	96	100
M. clarki	214633	3	102	96	100	100	110	100	101	99	100	100	100	97	98	93	100	100
M. clausus	214643	15	100	100	100(.93) 99(.07)	104	103	100	101	100	100	100	103	100	100(.03) 97(.97)	100	96	100
M. clenchi?	214652	1	102	100	99	100	103(.50) 100(.50)	100	102	99	100	100	100	97	97	96	102	100
M. edentatus	214653	3	100	99(.83) 95(.17)	100	100	103(.50) 100(.50)	100	103	100	100	100	100(.83) 97(.17)	97	103(.17) 100(.50) 98(.33)	95(.83) 93(.17)	96	100
M. elevatus	214655	18	100	96	100	100	103	100	102	100	100	100	100	97	100(.22) 97(.78)	97	96	103(.03) 100(.97)
M. ferrissi	214659	4	100	99	100	104	106	100	103	99	100	110	97	97	97(.50) 95.5(.50)	97	97	100
M. indianorum	214665	4	100	96	100	100	103	100	103	99	100	107	100	97	103(.25) 99(.75)	95	100	100
M. inflectus	214666	22	100	99	100	100(.75) 98(.25)	103	100	104	98	100	100	97	97	100(.54) 98(.46)	99(.80) 93(.20)	96	100(.70) 96(.30)
M. kalmianus	214682	5	102(.25) 100(.75)	96(.10) 95(.90)	100	100	103(.40) 100(.60)	100	103	100	100	100	103	97	100(.10) 95(.90)	97(.50) 93(.50)	96	101
M. kiowaensis	214684	4	100	100	100	100	103	100	103	100	100	100	90	97	98	97	100	100
M. laevior	214690	4	103	100	100	100	103(.12) 100(.88)	100	103	99	107(.75) 100(.25)	100	100	97	100(.12) 98(.25) 91(.63)	98(.88) 97(.12)	100	100(.12) 95(.88)
M. leatherwoodi	214692-3	2	100	100	100	100	103	100	103	99	105(.50) 100(.50)	100	110	97	92	101	100	105
M. magazinensis	214695	4	100	99	100	100	103	100	103	98	100	100	100	97	95	97	96	100

M. mitchellianus	214696	5	100	100	100	100	100	100	101	100	100	107	103(.10) 100(.90)	100	103(.10) 99(.90)	98	96	103(.80) 100(.20)
M. normalis	214979	22	100	100	100	100(.80) 98(.20)	100	100	102	100	100	100	100	97	96	99	102	100
M. orestes	214698	4	100	96	100	100	103	100	101	100	90	107(.38) 100(.62)	103(.25) 101(.75)	97	103(.38) 100(.38) 95(.24)	98(.12) 97(.88)	100	105(.12) 100(.88)
M. panselenus	214700	5	103	100	99	98	103	100	101	98	102(.20) 100(.80)	100	100	97(.90) 94(.10)	100(.40) 98(.60)	97	102	95
M. penn-sylvanicus	214703	1	100	96	100	100	100	100	103	100	100	100	103	97	97	99(.50) 96(.50)	100	100
M. perigraptus	214705	13	102	100(.38) 96(.62)	99	100	103	100	102	99	100	100	100	97	101(.42) 99(.58)	98(.54) 95(.46)	102	100
M. roemeri	214719	5	100	100	100	100	103	100	103	99	102	100	103	97	92(.10) 89(.90)	101	100	105
M. rugeli	uncat.	5	100	99	100	100	103	100	103	99	100	100	97	97	96(.60) 92(.40)	99	100(.10) 96(.90)	100
M. sanus	214727	3	100	100	100	100	105(.83) 103(.17)	100	101	100	100	100	103	97	100	100(.50) 95(.50)	100	105(.67) 100(.33)
M. sargentianus	214729	4	102	100	100	100	100	100	103	99	100	100	97	97	106(.12) 103(.88)	97(.50) 96(.50)	100	104(.25) 100(.75)
M. sayanus	214732	8	101(.12) 100(.88)	96	100	100(.19) 98(.81)	103(.75) 100(.25)	100	101	99	100	100(.94) 89(.06)	103	104(.06) 98(.94)	103(.62) 99(.19) 97(.19)	102(.06) 97(.94)	96	100(.81) 97(.06) 95(.13)
M. smithi	214738	3	100	99	100	100	100	100	103	99	100	100	100(.67) 97(.33)	97	103(.67) 100(.33)	97	96	100(.83) 96(.17)
M. subpalliatus	214740	5	100	100	100	100	106	100	103	98	100	101	97	97	95(.20) 90(.80)	95	100	100
M. thyroidus	214744	6	100	90	100	101	103	100	101	100	100	100	103	100	100(.58) 96.5(.42)	97	96	100
M. trossulus	214741	5	100	100	100	100	103	100	101	100	100	100	103	100	98(.30) 95(.70)	100(.40) 98(.60)	96	100
M. wetherbyi	214757	6	100	100	100	100	103	100	101	100	100	101	101	97	103(.58) 100(.25) 97(.17)	99(.25) 97(.42) 95(.33)	96	100
M. wheatleyi	214767	6	100	96	99	100	103	100	103	100	100	104(.22) 100(.78)	103(.22) 101(.78)	97	100	100	102(.56) 100(.44)	103(.11) 100(.89)
M. zaletus	214771	17	100	100	100	100	100	100	100	100	100	100	100(.79) 97(.21)	100	100(.88) 98(.12)	100(.91) 98(.09)	100	100(.82) 95(.18)
Ashmunella danielsi	214891	2	102	91	101	101	96	100	94	98	90	100	103	97	93.5	99	94	94

(continued)

TABLE 2. (continued)

Species	FMNH Catalogue Number	N	Sordh	Mdh-1	Mdh-2	Me	Icd	Pgd	Gd-1	Gd-2	Sod-1	Sod-2	Got-1	Got-2	Pgm	Lap	Mpi	Gpi
M. altivagus—2	214613	10	100	100	100	100	100	100	—	—	100	—	100	97	103(.40) 100(.60)	96	100	100
M. altivagus—3	214615	1	100	100	100	100	103	100	101	99	100	110	100	97	103	102	96	100
M. appressus—2	214619	10	102	100	100	—	103	100	—	—	90	—	100	97	99(.10) 97(.30) 95(.20) 91(.40)	98(.65) 96(.25) 93(.10)	96	100(.45) 95(.55)
M. appressus—3	214621	5	102	100	100	100	103	100	103	98	100(.50) 90(.50)	100	100	97	103(.10) 99(.60) 95(.30)	95	100	100(.20) 95(.80)
M. binneyanus—2	214626	1	100	96	100	100	103	100	103	100	100	107	100	97	99	97	100	100
M. chilhoweensis—2	214628	10	100	100	100	101	103	100	—	—	100	100	103	97	100(.30) 98(.70)	97	96	105(.15) 100(.85)
M. clarki—2	214632	11	102	96	100	—	106(.59) 103(.41)	103	—	—	100	—	103	100	98(.82) 97(.18)	96(.41) 93(.59)	100	100
M. clarki—3	214634	13	102	96	100	—	103	100	—	—	100	100	100	97	98	95	100	100
M. clausus—2	214644	12	97	100(.54) 96(.46)	100	100	103	100	102	99	100	100	103	100	100(.58) 97(.42)	100	100	100
M. clausus—3	214650	2	102(.50) 100(.50)	100(.50) 96(.50)	100(.50) 99(.50)	100	103(.75) 100(.25)	100	102	100(.50) 99(.50)	100	100	103(.50) 100(.50)	100(.50) 97(.50)	98(.50) 97(.50)	100(.50) 96(.50)	102(.50) 100(.50)	100
M. edentatus—2	214654	3	100	99	100	100	103(.83) 100(.17)	100	103	99	100	100	100	97	103(.50) 100(.50)	95(.83) 93(.17)	96	100
M. ferrissi—2	214657	10	100	99	100	—	106	100	—	—	100	—	97	97	97	97	97	100
M. ferrissi—3	214658	11	100	99	100	104	106	100	103	—	100	110	97	97	95.5	97	97	100(.73) 95(.27)
M. inflectus—2	214667	6	100	99	100(.92) 90(.08)	100	103	100	103	100	100	100	97	97	100(.25) 98(.33) 96(.42)	97(.50) 95(.50)	96	100(.92) 96(.08)
M. inflectus—3	214668	2	100	99	100	100	100	100	103	98	100	100	100	97	100(.75) 98(.25)	97	96	100
M. laevior—2	214687	10	103	100	100	100	100	100	—	—	100	—	100	97	98(.05) 95(.90) 91(.05)	100	100	100(.10) 95(.90)
M. laevior—3	214689	3	103	100(.67) 91(.33)	100	100	100	100	103	99	100	100	100	97	98(.83) 91(.17)	98	100	95
M. normalis—2	214966	4	100	100	100	100	100	100	102	100	100	100	100	97	98	101(.75) 97(.25)	102	100
M. panselenus—2	uncat.	1	103	100	99	98	103	100	101	98	100	100	100	97	98	97	102	100(.50) 95(.50)
M. perigraptus—2	214707	12	103	96	99	100	103	100	102	99	100	100	100	97	99(.62) 97(.38)	98(.38) 95(.62)	102	104(.04) 100(.96)

M. perigraptus—3	214710	5	102(.40) 97(.60)	100	99	100	103	100	102	99	100	100	100	97	99(.10) 97(.90)	98(.40) 95(.60)	102	105(.70) 95(.30)
M. roemeri—2	214718	2	100	100	100	100	103	100	103	99	102	100	103	97	89	101	100	105
M. rugeli—2	214720	11	100	99	100	100	103	100	104	98	100	100	97	97	100	95	96	100
M. rugeli—3	214725	5	100	99	100	100(.90) 98(.10)	102(.60) 95(.40)	100	103	99	100	100	100	97	100(.90) 96(.10)	97(.90) 89(.10)	96	100(.90) 96(.10)
M. sargentianus—2	214728	10	102	100	100	—	100	100	—	—	100	100	97	97	103(.70) 100(.30)	97(.85) 96(.15)	100	104(.40) 100(.60)
M. sayanus—2	214734	2	100	96	100	101	103	100	103	99	100	107(.50) 100(.50)	100	98	100(.75) 98(.25)	97	96	100
M. smithi—2	214736	10	100	99	100	—	103	100	—	—	100	100	100	97	103(.05) 100(.45) 98(.50)	97	96	100
M. smithi—3	214737	3	100	99	100	100	103	100	103	99	100	100	100	97	100(.67) 98(.33)	97(.17) 95(.66) 93(.17)	96	100
M. subpalliatus—2	214739	1	100	99	100	—	106	100	—	—	100	100	97	97	97(.50) 95(.50)	92	100	100
M. thyroidus—2	214743	9	100	96	100	101	103	100	103	100	100	100	103	100	100(.39) 98(.28) 97(.33)	97	96	103(.50) 100(.50)
M. thyroidus—3	uncat.	2	100	100	100	100	103	100	101	100	100	100	103	100	96	98	96	100
M. thryoidus—4	214750	2	100	90	100	101	103	100	101	100	100	100	103	100	103(.25) 95(.75)	100(.50) 97(.50)	96	100
M. thyroidus—5	214751	1	100	100	100	101	106(.50) 103(.50)	100	101	100	100	100	103	100	100(.50) 97(.50)	97	96	100
M. verus	214756	13	100	99	100	98	103	100	103	100	100	100	97(.96) 94(.04)	97	100(.15) 98(.23) 96(.62)	95	96	100
M. wheatleyi—2	214659	13	100	100(.42) 99(.58)	100	100	103	100	103	100	90	100	101	97	97	96	100	100
M. wheatleyi—3	214758	10	100	96	100	—	100	100	—	—	100(.60) 90(.40)	107	102	94	100(.60) 97(.40)	99(.40) 96(.60)	96	100
M. zaletus—2	214787	9	100	100	100	100	100	100	100	100	100	104(.22) 100(.78)	103(.22) 101(.78)	97	100	100	102(.56) 100(.44)	103(.11) 100(.89)
Total Alleles:	*Mesodon*	(Σ = 95)	5	6	3	4	8	2	5	3	3	5	6	5	16	12	4	8
	Ashmunella only	(Σ = 6)	0	0	1	0	1	0	1	0	0	0	0	0	1	0	1	1
	Total	(Σ = 101)	5	6	4	4	9	2	6	3	3	5	6	5	17	12	5	9

alleles were detected in the Mesodontini, and an additional six alleles were detected in the outgroup, *Ashmunella.* The most variable loci were Pgm and Lap, with 17 and 12 alleles. Icd and Gpi each had nine alleles; Mdh-1, Gd-1, and Got-1 each had six alleles; Sordh, Sod-2, Got-2 and Mpi each had five alleles; Mdh-2 and Me each had four alleles; Gd-2 and Sod-1 each had three alleles; and Pgd had two alleles. The allozymic data for the second outgroup, *Allogona profunda,* have been published in Emberton (1988: Table 2).

Heterozygosity within populations was extremely low. Most populations were monomorphic for all but two or three loci, with a maximum of four alleles per locus (Table 2).

Phylogenetic Analysis

The results of the first and preferred method of phylogenetic analysis only (see Discussion) are presented here. Results of the two alternative methods are presented in Appendices 2 and 3.

Removal of all autapomorphies from the data sets resulted in 21 informative genitalic transformations and 68 informative allozymic alleles. These 89 informative character states are identified in Table 3; their distributions among species are presented in Table 4.

The six Nelson consensus trees produced from these data are shown in Figures 29–34; their statistics are presented in Table 5. These trees differ in the degree to which the anatomical data are more heavily weighted than the biochemical data, these weights ranging from one to six. Because informative allozymic alleles were approximately three times as numerous as genitalic character states, Figure 31 (weight = three) approximately equates the **sets** of anatomical and biochemical data, and Figure 34 (weight = six) accords the **set** of anatomical data approximately twice the weight of the **set** of biochemical data.

The level of phylogenetic resolution of each of the six consensus trees (Figs. 29–34) depends at least partly on the number of trees from which it is constructed. Thus Figure 31, the least informative tree, is the consensus of 33 trees, the greatest number among the six consensuses (Table 4). One reason for this negative correlation between the number of trees and the phylogenetic resolution of their consensus is that the Nelson strict consensus method collapses clades that differ only in the placement of a single taxon (Hillis, 1987: fig. 2). In comparisons of Figures 29–34, the unfigured trees from which the Nelson consensuses were built were therefore consulted as well; these trees are available from the author upon request.

TABLE 3. Numbering of character states in Table 4, as used for phylogenetic analysis. All autapomorphic character states have been removed. For allozymic data (Table 2), all populations of each species have been pooled.

No.	Character State	No.	Character State
0	Transformation 1 (Fig. 26)	45	Gd2-98
1	Transformation 2 (Fig. 26)	46	Sod1-105
2	Transformation 3 (Fig. 26)	47	Sod1-100
3	Transformation 4 (Fig. 26)	48	Sod1-90
4	Transformation 8 (Fig. 26)	49	Sod2-110
5	Transformation 9 (Fig. 26)	50	Sod2-107
6	Transformation 11 (Fig. 26)	51	Sod2-101
7	Transformation 12 (Fig. 27)	52	Sod2-100
8	Transformation 14 (Fig. 27)	53	Got1-103
9	Transformation 16 (Fig. 27)	54	Got1-101
10	Transformation 17 (Fig. 27)	55	Got1-100
11	Transformation 19 (Fig. 27)	56	Got1-97
12	Transformation 20 (Fig. 27)	57	Got2-100
13	Transformation 21 (Fig. 27)	58	Got2-97
14	Transformation 24 (Fig. 27)	59	Pgm-103
15	Transformation 25 (Fig. 27)	60	Pgm-100
16	Transformation 26 (Fig. 28)	61	Pgm-99
17	Transformation 28 (Fig. 28)	62	Pgm-98
18	Transformation 30 (Fig. 28)	63	Pgm-97
19	Transformation 32 (Fig. 28)	64	Pgm-96.5
20	Transformation 33 (Fig. 28)	65	Pgm-96
21	Sordh-103	66	Pgm-95
22	Sordh-102	67	Pgm-92
23	Sordh-100	68	Pgm-89
24	Mdh1-100	69	Lap-104
25	Mdh1-99	70	Lap-102
26	Mdh1-96	71	Lap-101
27	Mdh1-95	72	Lap-100
28	Mdh1-91	73	Lap-99
29	Mdh2-100	74	Lap-98
30	Mdh2-99	75	Lap-97
31	Me-102	76	Lap-96
32	Me-100	77	Lap-95
33	Me-99	78	Lap-93
34	Me-97	79	Mpi-102
35	Icd-106	80	Mpi-100
36	Icd-103	81	Mpi-96
37	Icd-100	82	Mpi-94
38	Gd1-104	83	Gpi-105
39	Gd1-103	84	Gpi-104
40	Gd1-102	85	Gpi-103
41	Gd1-101	86	Gpi-100
42	Gd1-100	87	Gpi-96
43	Gd2-100	88	Gpi-95
44	Gd2-99		

The most robust clade is *Fumonelix,* which

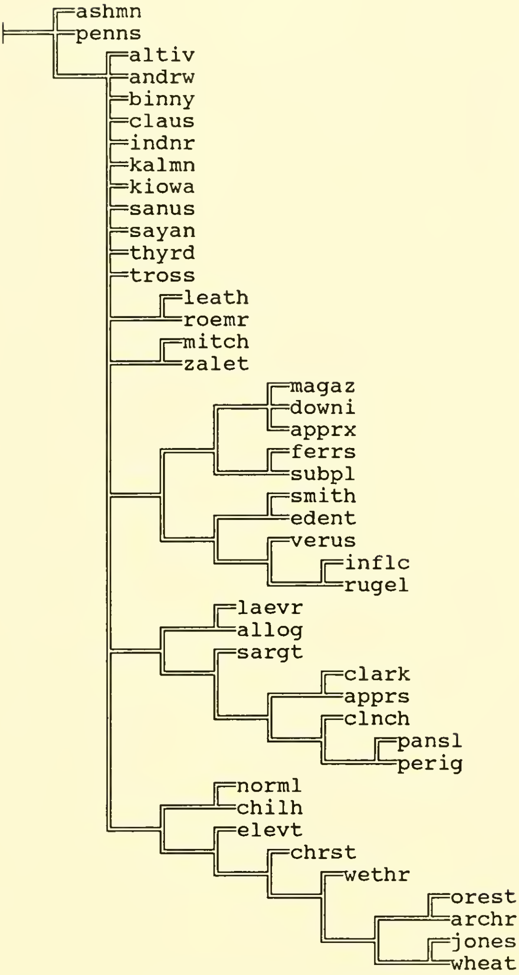


FIG. 29. Nelson consensus tree of 18 maximum-parsimony cladograms generated from data matrix in Table 4, with genitalic character states weighted the same as allozymic character states. See Table 5 for statistics, text for discussion.

appears consistently, regardless of the relative weights accorded anatomical and biochemical data (Figs. 29–34). All other clades vary with different weightings.

The second most robust clade is *Mesodon* (*Mesodon*). This subgenus shows the same phylogenetic structure in Figures 30–34. Of the 18 trees of which Figure 30 is the consensus, nine contain *M.* (*Mesodon*) intact, and nine differ in adding *M. zaletus* and *M. mitchellianus* at its terminus.

The third most robust clade is *Inflectarius* (*Inflectarius*). Placement of *I. downieanus* (see below) within this subgenus in the trees is considered an artifact of the lack of electrophoretic data for this species. *I.* (*Inflectarius*) is cohesive when anatomical characters are assigned weights of 1, 2, 3 and 4 [Figs. 29–32; Figure 31 divides the subgenus only because the alternative trees of which it is the consensus differ in placing *I. kalmianus* within (*Inflectarius*)]. Assignment of weights of 5 and 6 to anatomical states causes removal of *I. rugeli* from the subgenus, because of the plesiomorphic penial morphology of this species.

Mesodon (*Akromesodon*) is more strongly supported by the anatomical than by the electrophoretic data. The taxon occurs coherently

TABLE 4. Genitalic and allozymic data, with all autapomorphies removed, as used for phylogenetic analysis. Numbering of the 89 character states (listed in Table 3) starts at 0 in accord with the convention followed by Hennig86 (Farris, 1988). Absent = 0, present = 1 (genitalic transformation series are binary-coded).

		Character Number																	
Abbrev.	Species Name	0-4	5-9	10-14	15-19	20-24	25-29	30-34	35-39	40-44	45-49	50-54	55-59	60-64	65-69	70-74	75-79	80-84	85-89
asmun	*Ashmunella danielsi*	00000	00000	00000	00000	00100	00010	00100	00000	00000	01010	00110	00010	00000	00000	00010	00000	00100	0000
allog	*Allogona profunda*	00000	00000	00000	00000	00000	00001	01000	00000	00001	00000	00100	10010	00100	01010	10001	00000	10001	0100
altiv	*Mesodon altivagus*	00000	00000	00011	00010	10011	00001	00010	00100	00110	00100	00100	10011	10000	00000	00000	01000	10000	0100
andrw	*Mesodon andrewsae*	00000	01000	00011	00010	00011	00001	00010	01000	01001	00101	00010	10011	00000	00001	10000	01000	01010	0100
apprs	*Patera appressa*	00000	00000	00000	00011	00101	00001	00010	01001	00000	10110	00100	10011	01010	01010	00001	01110	11000	0101
apprx	*Inflectarius approximans*	11000	00000	00000	00000	00010	10001	00010	01001	00001	00100	00100	01010	00000	00000	00001	00000	01000	0100
archr	*Fumonelix archeri*	00000	10000	11100	01000	0????	?????	?????	?????	?????	?????	?????	?????	?????	?????	?????	?????	?????	????
binny	*Patera binneyana*	00000	00000	00000	00000	00010	01001	00010	01001	00011	00100	10000	10010	01000	01000	00000	10000	10000	0100
chilh	*Mesodon chilhoweensis*	00000	00000	00010	00000	00011	00001	01100	01000	10010	00100	00110	00010	10100	01000	00000	10000	11010	0101
chrst	*Fumonelix christyi*	00001	00000	10000	00100	01001	00001	00010	00000	10010	00100	00101	00010	01010	01000	00010	10000	01000	0100
clark	*Patera clarki*	00000	00000	00000	00000	00100	01101	00010	11000	01001	00100	00110	10110	00110	00000	00000	01110	10000	0100
claus	*Mesodon clausus*	00000	00000	00010	10010	10011	01001	11010	01000	11011	00100	00110	00100	10100	00000	00100	00000	11100	0100
clnch	*Patera clenchi*	00000	00000	00000	00000	00101	00000	10010	01100	10001	00100	00100	10010	00010	00000	00000	01001	00000	0100
downi	*Inflectarius downieanus*	11000	00000	00000	00000	0????	?????	?????	?????	?????	?????	?????	?????	?????	?? ???	?????	?????	?????	????
edent	*Inflectarius edentatus*	00000	00000	00000	00000	00010	10101	00010	01101	00011	00100	00100	11011	10100	00000	00000	00110	01000	0100
elevt	*Mesodon elevatus*	00000	00000	00000	00011	00010	01001	00010	01000	10010	00100	00100	10010	10010	00000	00000	10000	01000	1100
ferrs	*Inflectarius ferrissi*	00110	00000	00000	00000	00010	10001	01000	10001	00001	00101	00000	01010	00010	00000	00000	10000	00000	0101
indnr	*Patera indianorum*	00000	00000	00000	00000	00010	01001	00010	01001	00001	00100	10000	10011	01000	00000	00000	00100	10000	0100
inflc	*Inflectarius inflectus*	10100	00000	00000	00000	00010	10001	00011	01111	00010	10100	00100	11010	10100	10000	00010	10110	01000	0110
jones	*Fumonelix jonesiana*	00001	00000	11100	01000	0????	?????	?????	?????	?????	?????	?????	?????	?????	?????	?????	?????	?????	????
kalmn	*Inflectarius kalmianus*	00000	00000	00000	00000	00110	01101	00010	01101	00010	00100	00110	00010	10000	01000	00000	10010	01000	0000
kiowa	*Patera kiowaensis*	00000	00000	00000	00000	00011	00001	00010	01001	00010	00100	00100	00010	00100	00000	00000	10000	10000	0100

laevr	*Patera laevior*	00000	00000	00000	00000	01001	00011	00010	01101	00001	00100	00100	10010	10100	01010	00101	10000	10000	0101
leath	*Patera leatherwoodi*	00000	00100	00000	00000	00011	00001	00010	01001	00001	01100	00100	00010	00000	00100	01000	00000	10010	0000
magaz	*Inflectarius magazinensis*	11000	00000	00000	00000	00010	10001	00010	01001	00000	10100	00100	10010	00000	01000	00000	10000	01000	0100
mitch	*Mesodon mitchellianus*	00000	00000	00010	00011	00011	00001	00010	00100	01010	00100	10010	10101	01000	00000	00001	00000	01000	1100
norml	*Mesodon normalis*	00000	01000	00011	00000	00011	00001	00011	00100	10010	00100	00100	10010	00100	10000	01010	10001	00000	0100
orest	*Fumonelix orestes*	00000	10000	11100	01000	00010	10001	00010	01000	01010	00010	10111	00011	10000	01000	00001	10000	10010	0100
pansl	*Patera panselena*	00000	00000	00000	00000	01001	00000	10001	01000	01000	10100	00100	10010	10100	00000	00000	10001	00000	0101
penns	*Patera pennsylvanica*	00000	00001	00000	00000	00010	01001	00010	00100	00010	00100	00110	00010	00010	00000	00010	01000	10000	0100
perig	*Patera perigrapta*	00000	00000	00000	00000	01101	01000	10010	01000	11001	00100	00100	10010	01010	00000	00001	00101	00010	0101
roemr	*Patera roemeri*	00000	00100	00000	00000	00011	00001	00010	01001	00001	00000	00110	00010	00000	00100	01000	00000	10010	0000
rugel	*Inflectarius rugeli*	00110	00010	00000	00000	00010	10001	00011	01011	00001	10100	00100	11010	10000	10100	00010	10100	11000	0110
sanus	*Mesodon sanus*	00000	00000	00010	10010	10011	00001	00010	01000	01010	00100	00110	00010	10000	00000	00100	00100	10010	0100
sargt	*Patera sargentiana*	00000	00000	00000	00000	00101	00001	00010	00101	00001	00100	00100	01011	10000	00000	00000	11000	10001	0100
sayan	*Mesodon sayanus*	00000	00000	00010	00000	00010	01001	00111	01101	01001	00100	10110	10001	11110	00000	10000	10000	01000	0101
smith	*Inflectarius smithi*	00000	00000	00000	00000	00010	10001	00010	01101	00001	00100	00100	11011	10100	00000	00000	10110	01000	0110
subpl	*Inflectarius subpalliatus*	00110	00010	00000	00000	00011	10001	00010	10001	00000	10100	01100	01010	00010	01000	00000	00100	10000	0100
thyrd	*Mesodon thyroidus*	00000	00000	00010	10010	10011	01001	00110	11001	01010	00100	00110	00101	10111	11000	00101	10000	01000	1100
tross	*Mesodon trossulus*	00000	00000	00010	10010	10011	00001	00010	01000	10010	00100	00110	00100	00100	01000	00101	00000	01000	0100
verus	*Inflectarius verus*	00000	00000	00000	00000	00010	10001	00001	01001	00010	00100	00100	01010	10100	10000	00000	00100	01000	0100
wethr	*Fumonelix wetherbyi*	00000	00000	11000	00000	00011	00001	00010	01000	01010	00100	01001	00011	10010	00000	00010	10100	01000	0100
wheat	*Fumonelix wheatleyi*	00001	00000	11100	01100	00011	11001	10010	01101	00010	00110	10101	00011	11010	00000	00010	01000	11000	0100
zalet	*Mesodon zaletus*	00000	00000	00010	00011	00011	00001	00011	00100	00110	00100	00110	11101	10111	01011	00101	01001	10000	1101

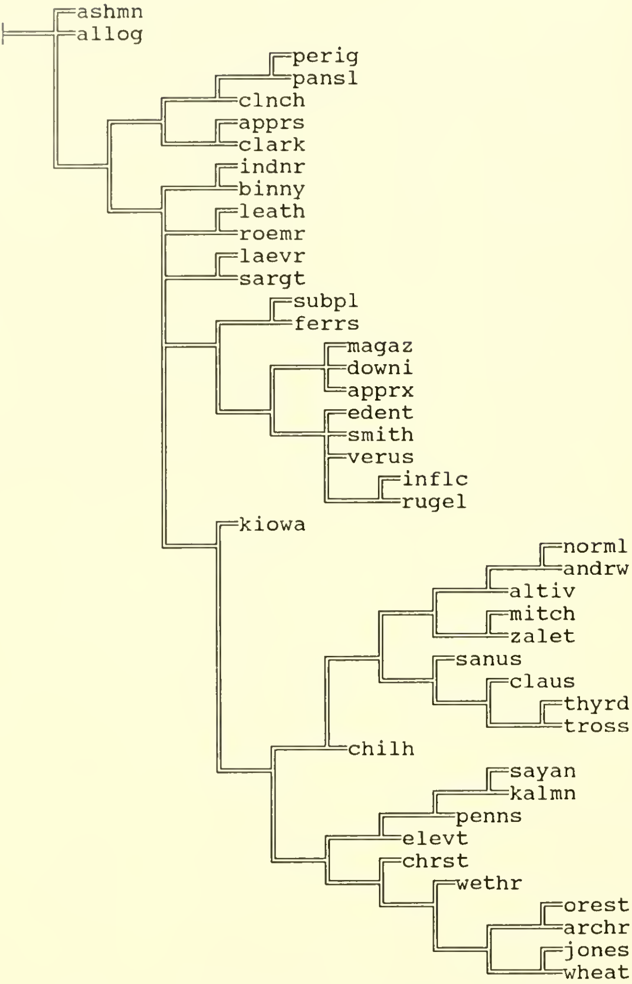


FIG. 30. Nelson consensus tree of 15 maximum-parsimony cladograms generated from data matrix in Table 4, with genitalic character states assigned twice the weight of allozymic character states. See Table 5 for statistics, text for discussion.

in Figures 32–34 (except for the incursion of *Patera appressa*, discussed below). In Figure 30, the taxon is intact except for the removal of *M. elevatus;* of the 33 trees of which Figure 31 is the consensus, *M.* (*Akromesodon*) occurs with *M. elevatus* in three, and without *M. elevatus* in 30. Only in Figure 29, in which anatomical and electrophoretic characters have equal weight, does *M.* (*Akromesodon*) break down, the only consistent elements being the pairing of *M. zaletus* with *M. mitchellianus,* although other elements of the subgenus recur among the 18 trees of which Figure 29 is the consensus.

Patera (*Patera*) appears intact and monophyletic (except for the incursion of *Allogona* and *Patera clenchi,* discussed below) only in Figure 29, in which anatomical and allozymic character states receive equal weight. It appears intact and paraphyletic in Figures 30 and 31 (because rotation of branches on any given node does not change the topologies of these trees), in the latter of which anatomical data as a whole are given the same weight as allozymic data as a whole. With increased weighting of anatomy (Figs. 32–34), however, *P. appressa* moves from *P.* (*Patera*) to *Mesodon* (*Akromesodon*). This move is inter-

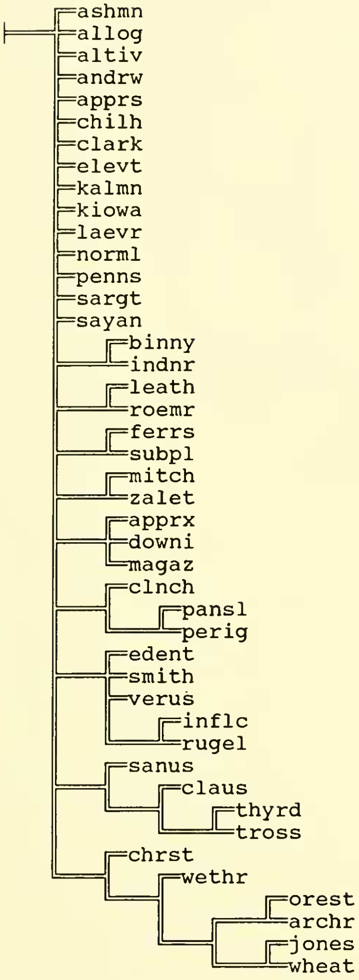


FIG. 31. Nelson consensus tree of 33 maximum-parsimony cladograms generated from data matrix in Table 4, with genitalic character states assigned three times the weight of allozymic character states. See Table 5 for statistics, text for discussion.

preted as the result of anatomical convergence between *P. appressa* (Fig. 19c) and *M. elevatus* (Fig. 4f–j). Less drastic breakdown of *P.* (*Patera*) upon heavy weighting of anatomical data—the isolation of *P. sargentiana* in Figure 33 and of *P. clarki* in Figure 34—are also assumed to reflect genitalic convergence.

In all of the 18 trees of which Figure 29 is the consensus, *P.* (*Vesperpatera*) (with the exception of *P. clenchi,* discussed below) appears paraphyletically at the base of a clade leading to *P.* (*Patera*). The only reason this basal position does not occur in Figure 29 is that there is an incursion in nine of the 18 trees of *M. sayanus* and *M. andrewsae* as a sister group to *P. indianorum;* owing to the strict-consensus algorithm, this migrating unit causes the entire *Patera* clade to collapse into a polychotomy that belies much of the phylogenetic information.

Similarly, (*Vesperpatera*) occurs paraphyletically in all 15 trees from which Figure 30 is derived, but is introgressed by *P. sargentiana* and *P. laevior* in 11 of the trees. The 33 trees comprising Figure 31 have *P.* (*Vesperpatera*) paraphyletic and intact in six, interrupted by either *P. sargentiana* and *P. laevior* or by the group *P. sargentiana, Inflectarius subpalliatus* and *I. ferrissi. Patera* (*Vesperpatera*) occurs phylogenetically intact and paraphyletic in Figure 32, but interrupted by the group *P. sargentiana, Inflectarius subpalliatus, I. ferrissi* and *I. rugeli* in Figure 33. In the 30 trees constituting Figure 34, the majority have *Patera* (*Vesperpatera*) paraphyletic and intact. The close affiliation of *P. "clenchi"* with *P. perigrapta* throughout the consensus trees strongly supports the initial thought that the single electrophoresed juvenile was really a misidentified *P. perigrapta,* which was extremely common at that site (Calico Rock, Arkansas). *P. clenchi* is tentatively placed in *P.* (*Vesperpatera*), with which it agrees not only in genital morphology but also in shape of shell and geographical distribution. The relative isolation of *P. kiowaensis* within *P.* (*Vesperpatera*) is due in large part to its sharing two allozymic alleles with many species of *Mesodon* and *Fumonelix,* as well as with other species (see especially Figure 30). Because these bands are adjacent on the electrophoretic zymograms, *P. kiowaensis* might have only one of them, and a misinterpretation of one or more gels might have assigned it two.

The *Inflectarius subpalliatus-I. ferrissi* clade is a consistent feature of Figures 29–32. Only in Figures 33 and 34 is it divided by *I. rugeli,* which has a plesiomorphic genital morphology similar to that of *I. subpalliatus,* presumably by atavistic parallelism.

Mesodon (*Appalachina*) is supported more by anatomy than by allozymes, for it occurs in Figures 32–34, but not in Figures 29–31. Of the 33 trees from which Figure 31 is derived, *M.* (*Appalachina*) appears in 15; in two other configurations its two species are separated by *Mesodon normalis* and by a clade consisting of *M. elevatus, Patera pennsylvanica* and

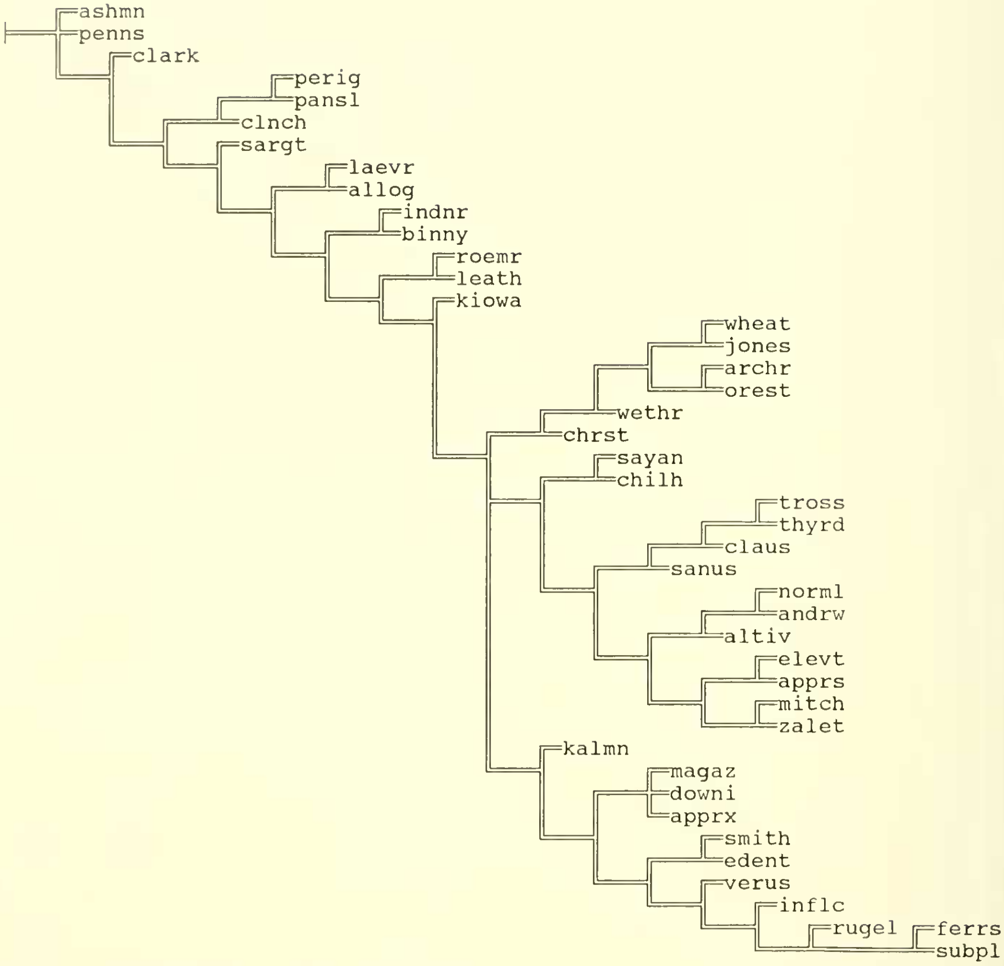


FIG. 32. Nelson consensus tree of 6 maximum-parsimony cladograms generated from data matrix in Table 4, with genitalic character states assigned four times the weight of allozymic character states. See Table 5 for statistics, text for discussion.

Inflectarius kalmianus. The latter configuration obtains in Figure 30. In the 18 trees from which Figure 29 was computed, *Mesodon sayanus* is consistently split, with *M. chilhoweensis* always paired with *M. normalis,* and with *M. sayanus* paired with either *M. andrewsae* or *Inflectarius kalmianus*.

Inflectarius (*Hubrichtius*) is the most tentative taxon in this study. In the absence of electrophoretic data the position of *I. downieanus* in all consensus trees (Figs. 29–34) within *I.* (*Inflectarius*) serves only as evidence of its generic placement. Pairing this species with *I. kalmianus* is based solely upon the great conchological similarity of these two species.

Patera (*Ragsdaleorbis*) is the only monospecific subgenus in this revision. *P. pennsylvanica* appears isolated as the most plesiomorphic species of the Mesodontini in Figures 29, 32 and 33. In other censensus trees, it appears either between *Mesodon elevatus* and *Inflectarius kalmianus* (Fig. 30), or paired with *Patera clarki*.

Because it is not divided into subgenera, further discussion the integrity of the genus *Fumonelix* in the cladograms is unnecessary. Inclusion of the *I. subpalliatus-I. ferrissi* clade in the genus *Inflectarius* is required by Figures 29, 30 and 32; by 30 of the 33 trees from which Figure 31 was generated; and by the

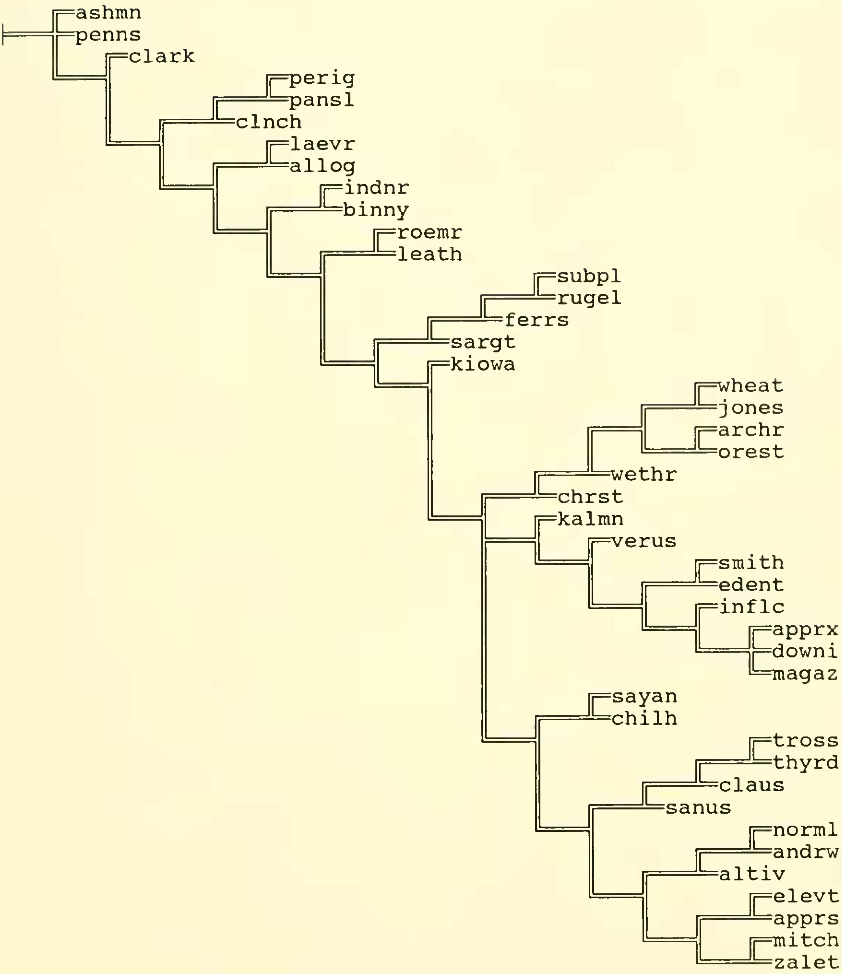


FIG. 33. Nelson consensus tree of 6 maximum-parsimony cladograms generated from data matrix in Table 4, with genitalic character states assigned five times the weight of allozymic character states. See Table 5 for statistics, text for discussion.

affiliation of this subgenus with *I. rugeli* in Figures 33 and 34. Two facts support the inclusion of the problematic *I.* (*Hubrichtius*) in *Inflectarius.* One is the consistent association of *I. downieanus* (based upon genital morphology only, in the absence of pertinent allozymic data) with *I. magazinensis* and *I. approximans* (Figs. 29–34). The other is the occurrence of *I. kalmianus* at the base of *I.* (*Inflectarius*) in Figures 32–34 and in all of the 18 trees from which Figure 29 was generated (not apparent in Figure 29 because in six of the 18 trees, *Mesodon sayanus* is paired with *Inflectarius kalmianus*), as well as within *I.* (*Inflectarius*) in three of the 33 trees of which Figure 31 is the consensus. The alternative positions of *I. kalmianus* in Figure 30 and in the majority of the trees comprising Figure 31 are tentatively deemed spurious and due to homoplasies.

The type species of the genus *Mesodon* is *M. thyroidus; M.* (*Mesodon*) therefore belongs within the genus *Mesodon a priori. M.* (*Akromesodon*) also clearly belongs in *Mesodon* because it or the majority of its species form the sister group of (or rarely are intermixed with) *M.* (*Mesodon*) in all the trees from which Figures 29 and 31 were computed, and in Fig-

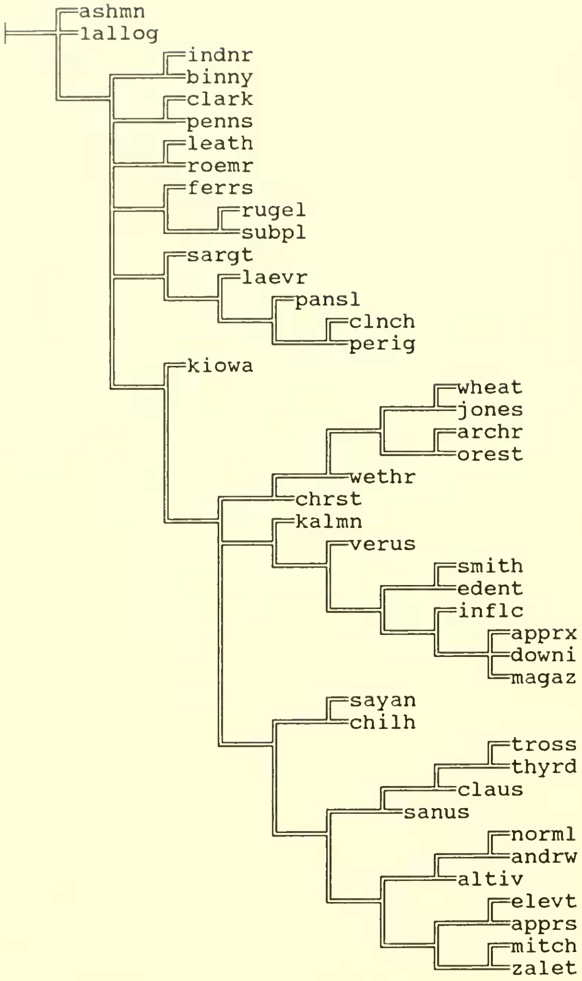


FIG. 34. Nelson consensus tree of 30 maximum-parsimony cladograms generated from data matrix in Table 4, with genitalic character states assigned six times the weight of allozymic character states. See Table 5 for statistics, text for discussion.

ures 30 and 32–34. *M.* (*Appalachina*) appears at the base of the clade *M.* (*Mesodon*) *M.* (*Akromesodon*) in Figures 32–34 and in 18 of the 33 trees comprising Figure 31. One member of the subgenus, *M. chilhoweensis*, retains this position in Figure 30 and in the additional trees comprising Figure 31; although it assumes another cladistic position in Figure 29, this species is still paired with *Mesodon normalis.* In 12 of the 18 trees of which Figure 29 is the consensus, *M. sayanus* is paired with *M. andrewsae. M.* (*Appalachina*) therefore is placed in *Mesodon* as its most plesiomorphic member. The association of *M. sayanus* with *I. kalmianus* in Figure 30 is expected, inasmuch as these two species are the plesiomorphic members of their respective clades, *Inflectarius* and *Mesodon.*

Inclusion of *P.* (*Vesperpatera*) in *Patera* (of which *P. appressa* is the type species) is required by its close association with *P.* (*Patera*) *in all trees, including those comprising Figures* 29 and 31 (in which resolution is lost owing to the strict consensus algorithm). The monospecific *P.* (*Ragsdaleorbis*) is placed tentatively in this genus as well, owing to its being plesiomorphic with respect to the rest of *Patera* in Figures 32 and 33, and in three of

TABLE 5. Statistics on the six cladograms in Figures 29–34, produced by Hennig86 (Farris, 1988) from 89 informative characters (21 genitalic, 68 allozymic) of the Mesodontini. Column headings refer to sequence of commands in this software program: "ccode /1" to "ccode /6" assign weights to genitalic character states (numbers "0" to "20") of one to six times the weights of allozymic alleles; "mhenning*" trees are produced by single passes through data, and branch-swapping is then applied to them; "bb*" subjects these same trees to further branch-swapping, and outputs all trees of greatest discovered parsimony; "nelsen" produces a Nelson (1979) strict consensus tree from the set of most parsimonious trees. C.I. = consistency index, R.I. = retention index (Farris, 1989).

ccode	mhennig*				bb*				nelsen	
/# 0.20	#Trees	Length	C.I.	R.I.	#Trees	Length	C.I.	R.I.	Length	Fig. #
1	1	374	23	47	18	374	23	47	450	29
2	1	409	26	50	15	409	26	50	417	30
3	2	443	29	53	33	443	29	53	554	31
4	4	473	32	56	6	472	32	56	473	32
5	3	500	34	59	6	499	34	59	500	33
6	1	528	36	61	30	527	36	61	533	34

the 33 trees from which Figure 31 is constructed; and owing to its affiliation with *P. clarki* in Figure 34. The association of *P. pennsylvanica* with *Inflectarius kalmianus* in Figure 30 and in 30 of the 33 trees comprising Figure 31 is enigmatic.

With respect to phylogenetic relationships among the four genera, *Mesodon* and *Fumonelix* appear as sister groups in Figure 30, in 30 of the 33 trees comprising Figure 31, in half of each of the sets of six trees comprising Figures 32 and 33, and in half of the 30 trees from which Figure 34 was derived. In Figure 29 as well, all three species at the base of *Fumonelix* are members of *Mesodon*. *Patera* seems to be the most plesiomorphic genus in the Mesodontini: it occupies this position in Figures 30, 31–34, in 31 of the 33 trees constituting the consensus of Figure 31, and in seven of the 18 trees from which Figure 29 was constructed. Phylogenetically, then, *Inflectarius* falls between *Patera* and *Fumonelix-Mesodon.*

The result of these comparisons of the cladistic analyses is the following classification. Presentation of this phylogenetic hypothesis in the form of a tree is deferred to the consideration of conchological evolution.

Revised Classification

The complete systematic review is given in Appendix 1. Here the classification is simply outlined, with the genera, subgenera, and groups of species arranged phylogenetically, from most plesiomorphic to most apomorphic. Species are listed alphabetically within groups. An asterisk denotes the type species of each genus and subgenus.

Patera Albers, 1850
  Patera (*Ragsdaleorbis*) Webb, 1954b
      pennsylvanica (Green, 1827)*
  Patera (*Vesperpatera*) *subgen. nov.*
    binneyana group
      binneyana (Pilsbry, 1899)
      clenchi (Rehder, 1932)
      indianorum (Pilsbry, 1899)
      kiowaensis (Simpson, 1888)
    roemeri group
      leatherwoodi (Pratt, 1971)
      roemeri (Pfeiffer, 1848)*
  Patera (*Patera*)
    perigrapta group
      penselena (Hubricht, 1976)
      perigrapta (Pilsbry, 1894b)
    appressa group
      appressa (Say, 1821)*
      laevior (Pilsbry, 1940)
      sargentiana (Johnson & Pilsbry, 1892)
    clarki group
      clarki (Lea, 1858)
Inflectarius Pilsbry, 1940
  Inflectarius (*Hubrichtius*) subgen. nov.
      downieanus (Bland, 1861)
      kalmianus (Hubricht, 1965)*
  Inflectarius (*Inflectarius*)
    edentatus group
      edentatus (Sampson, 1889)
      magazinensis (Pilsbry & Ferriss, 1907)
    smithi group
      smithi (Clapp, 1905)
    inflectus group
      approximans (Clapp, 1905)
      inflectus (Say, 1821)*

        rugeli (Shuttleworth, 1852)
        verus (Hubricht, 1954)
    ferrissi group
        ferrissi (Pilsbry, 1897)
        subpalliatus (Pilsbry, 1893)
Fumonelix gen. nov.
    christyi group
        christyi (Bland, 1860)
    wetherbyi group
        wetherbyi (Bland, 1874)
    wheatleyi group
        archeri (Pilsbry, 1940)
        jonesiana (Archer, 1938)
        orestes (Hubricht, 1975)
        wheatleyi (Bland, 1860)*
Mesodon Férussac, 1821
  Mesodon (*Appalachina*) Pilsbry, 1940
        chilhoweensis (Lewis, 1870)
        sayanus (Pilsbry, in Pilsbry & Ferriss, 1906)*
  Mesodon (*Aphalogona*) Webb, 1954b
        elevatus (Say, 1821)*
        mitchellianus (Lea, 1838)
        zaletus ("Say" Binney, 1837)
  Mesodon (*Akromesodon*) subgen. nov.
        altivagus (Pilsbry, 1900)
        andrewsae (Binney, 1879)
        normalis (Pilsbry, 1900)*
  Mesodon (*Mesodon*)
        clausus (Say, 1821)
        sanus (Clench & Archer, 1933)
        thyroidus (Say, 1817)*
        trossulus (Hubricht, 1966)

Table 6 permits comparison of this classification with those of Pilsbry (1940), based on shell morphology; and of Webb (1954b, 1968a, 1968b, 1983), based on genital anatomy and behavior.

Conchological Variation

Conchological illustrations of 39 of the 42 species of Mesodontini are presented in Figures 35–50. Of the three species not illustrated, *Fumonelix archeri* and *Inflectarius verus* have extremely restricted ranges, and the shell of *Patera indianorum* resembles that of *P. binneyana,* except for its umbilicus, which is closed to narrowly chinked. Both *F. archeri* and *P. indianorum* are illustrated in Pilsbry (1940), whose monograph should be consulted for an understanding of variation within species in shell morphology. An illustrated key to most of the species is contained in Burch (1962). Range maps are available both in this paper (Fig. 51) and in greater detail and with ecological notes in Hubricht (1985). It is important to remember in identifying any shell of the Mesodontini that many species of the Triodopsini have closely convergent shells (see Emberton, 1988).

Patterns of Genitalic Evolution

The ranges of the 42 species of the Mesodontini are presented in Fig. 51. These maps were compiled from Hubricht (1985), with a correction for *Mesodon mitchellianus.* The ranges of *Inflectarius verus* and *Mesodon trossulus* are from Hubricht (unpublished), and the range of *M. altivagus* is from data in Pilsbry (1940).

These maps were used to assess the relationships in geographic ranges among pairs of sister taxa, which were also compared in genital morphology (Figs. 2–25). The results, based on 29 pairs of sister taxa, are presented in Table 7. Of the four pairs showing a great difference in penial morphology, three had parapatric ranges and one had an allopatric range. Thirteen pairs of sister taxa were deemed moderately different in genital morphology, and of these, four were allopatric, two were peripatric, four were parapatric and three were sympatric. Of eight pairs of sister taxa whose genitalia differ only slightly four or five were mostly peripatric, one or two showed some allopatry and two were sympatric. Peripatry predominated over sympatry (three to one) among the four pairs of sister taxa judged not to differ in their penial morphologies.

The tests for character displacement in reproductive organs at the level of population are summarized in Table 8. In none of these 16 comparisons was there any detectable difference in penial morphology between allopatric and sympatric populations.

Patterns of Shell Evolution

Figure 52 shows the phylogenetic pattern of shell morphology among all known species of the Mesodontini (these are the only illustrations in this paper of the shells of *Patera indianorum, Inflectarius verus* and *Fumonelix archeri*). There is an evolutionary pattern of relative conchological stasis within subgenera. In general, each subgenus is characterized by a distinct shell form: shells of *Mesodon* (*Akromesodon*) (Figs. 35c–f, 36e–f) are large, globose, imperforate, toothless and hairless; those of *Mesodon* (*Mesodon*) (Figs.

TABLE 6. Revised supraspecific classiciation compared with classifications of Pilsbry (1940) and of Webb (1954b, 1968a, 1968b, 1983).

This Classification	Previous Classifications	
	Subgeneric Placement within *Mesodon*	
Genus, Subgenus, Species	Pilsbry	Webb
Fumonelix		
archeri	*Mesodon*	—
christyi	*Mesodon*	*Ragsdaleorbis*
jonesiana	*Patera*	—
orestes	—	—
wetherbyi	*Patera*	—
wheatleyi	*Mesodon*	—
Inflectarius		
Hubrichtius		
downieanus	*Mesodon*	—
kalmianus	—	—
Inflectarius		
approximans	*Inflectarius*	—
edentatus	*Inflectarius*	—
ferrissi	*Mesodon*	—
inflectus	*Inflectarius*	*Inflectarius*
magazinensis	*Inflectarius*	—
rugeli	*Inflectarius*	—
smithi	*Inflectarius*	—
Inflectarius		
Inflectarius		
subpalliatus	*Patera*	—
verus	—	—
Mesodon		
Akromesodon		
altivagus	*Mesodon*	—
andrewsae	*Mesodon*	—
normalis	*Mesodon*	—
Aphalogona		
elevatus	*Mesodon*	*Aphalogona*
mitchellianus	*Mesodon*	—
zaletus	*Mesodon*	*Aphalogona*
Appalachina		
chilhoweensis	*Appalachina*	—
sayanus	*Appalachina*	—
Mesodon		
clausus	*Mesodon*	*Mesodon*
sanus	*Mesodon*	—
thyroidus	*Mesodon*	*Mesodon*
trossulus	—	—
Patera		
Patera		
appressa	*Patera*	*Patera*
clarki	*Mesodon*	—
laevior	*Patera*	—
panselena	—	—
perigrapta	*Patera*	—
sargentiana	*Patera*	*Patera*
Ragsdaleorbis		
pennsylvanica	*Mesodon*	*Ragsdaleorbis*
Vesperpatera		
binneyana	*Mesodon*	—
clenchi	*Mesodon*	—
indianorum	*Mesodon*	—
kiowaensis	*Mesodon*	*Patera*
leatherwoodi	—	—
roemeri	*Mesodon*	—

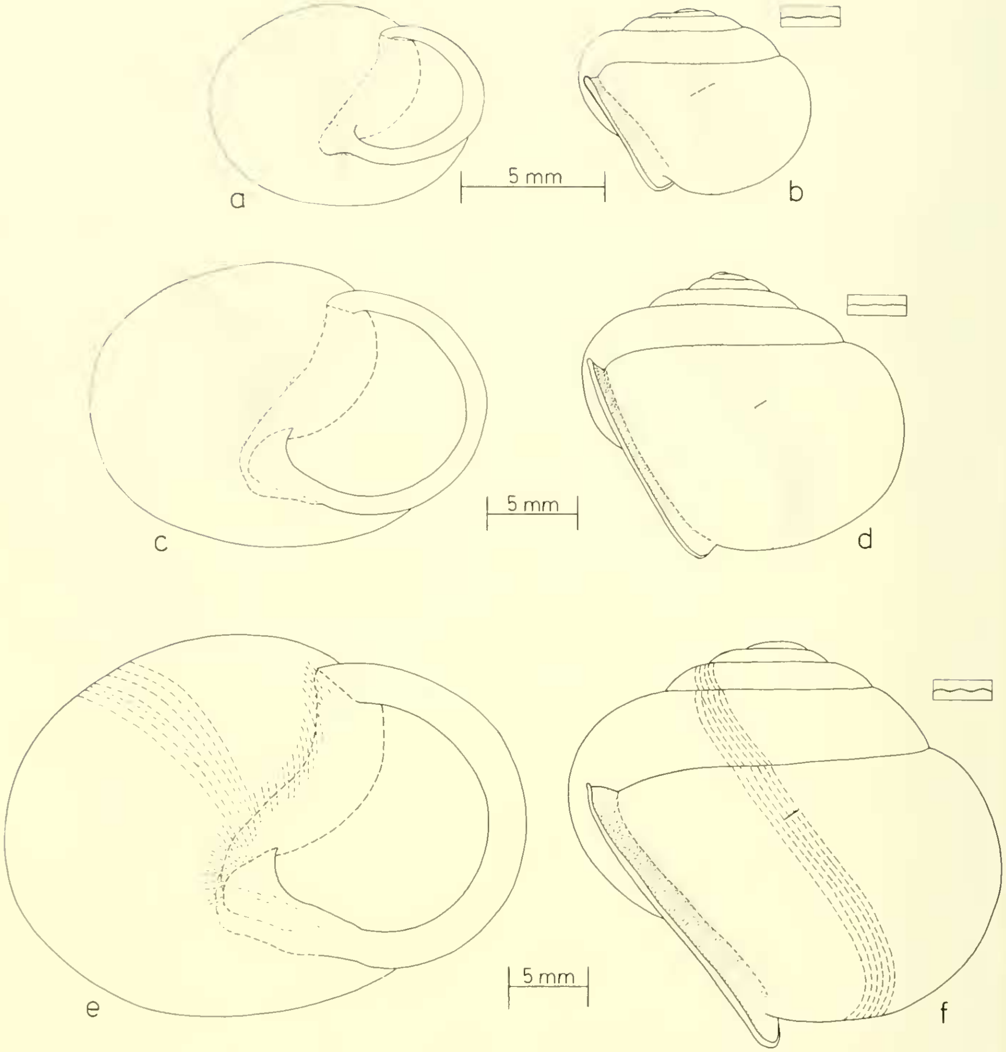


FIG. 35. Shells. a,b. *Inflectarius kalmianus,* GS-116 #18. c,d. *Mesodon andrewsae,* Roan Mountain, GS-11 #1. e,f. *Mesodon normalis,* SC-158 #2.

36a–d, 37c–f) are generally medium-sized, globose, with a creviced umbilicus, toothless and hairless; those of *Mesodon* (*Aphalogona*) (Figs. 37a,b, 38) are generally large, globose, imperforate, bearing a single pronounced parietal tooth and hairless; shells of *Mesodon* (*Appalachina*) (Fig. 39) are large, subglobose, broadly umbilicate, with a baso-columellar tooth or node and hairless; those of *Fumonelix* (Figs. 40c–d, 41, 42) are generally small, subglobose, imperforate, with a single parietal tooth and hairless; shells of *Inflectarius* (*Inflectarius*) (Figs. 40a,b,e,f, 43, 44) are generally small, subglobose, imperforate, tridentate (with parietal, palatal, and basal teeth) and hairy; those of *Inflectarius* (*Hubrichtius*) (Figs. 35a,b, 45a,b) are small, globose, imperforate, toothless and hairless; shells of *Patera* (*Patera*) (Figs. 46, 47, 48c–d) are generally medium-sized, depressed, imperforate, with a blade-like parietal tooth and a long basal lamella and hairless; those of *Patera* (*Vesperpatera*) (Figs. 48a,b, 49, 50) are generally medium-sized, depressed, with a creviced to open umbilicus, toothless and hairless; and shells of *Patera* (*Ragsdaleorbis*)

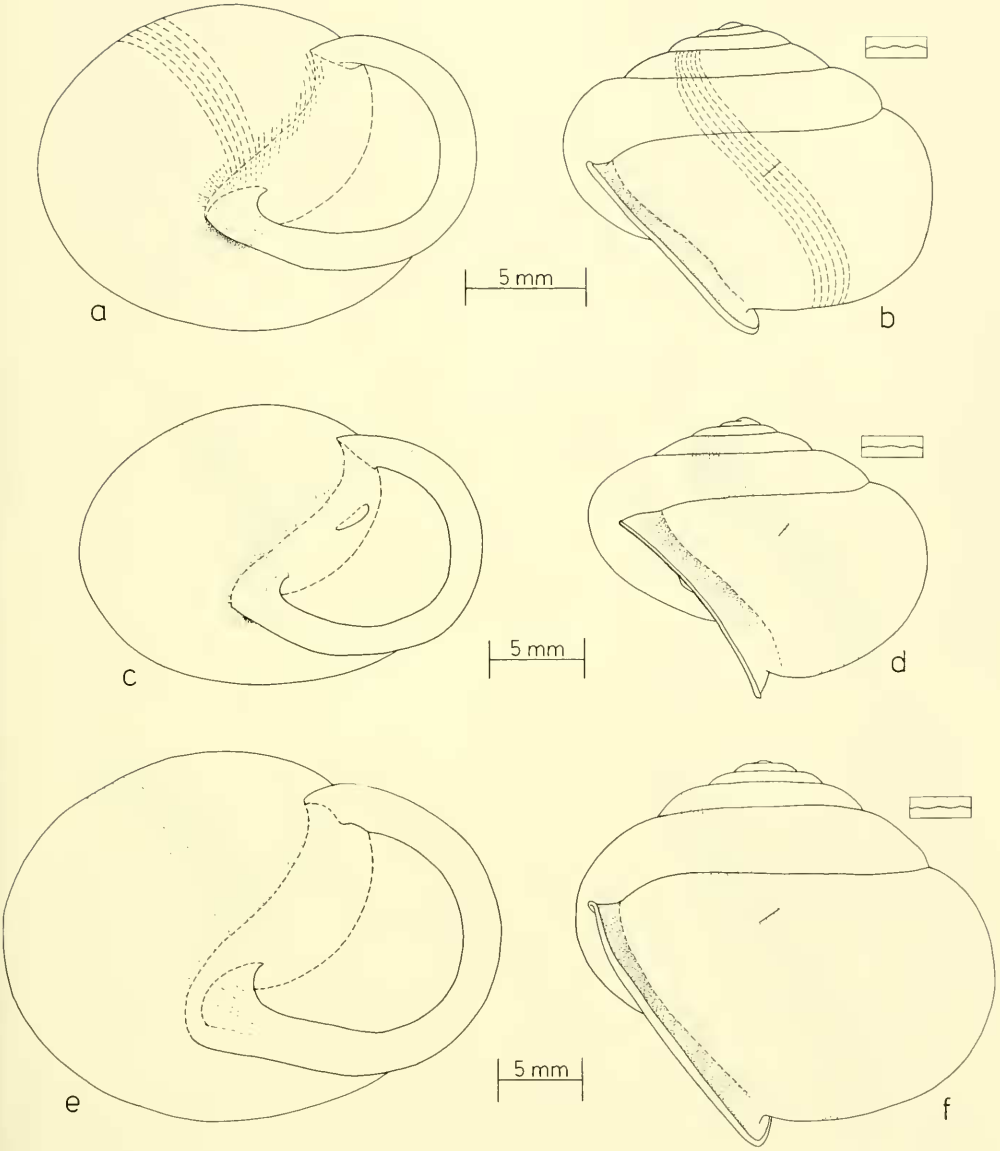


FIG. 36. Shells. a,b. *Mesodon sanus*, GS-103 #8. c,d. *Mesodon thyroidus*, GS-63 #11. e,f. *Mesodon altivagus*, SC-144 #7.

(Figs. 45c–d) are medium-sized, globose, imperforate, toothless and hairless.

Most of the shapes of shells of the various subgenera are unique and distinctive within the Mesodontini (but converge on those of other groups; see below). The resemblance is rather close, however, among *Patera* (*Ragsdaleorbis*), *Inflectarius* (*Hubrichitus*), *Mesodon* (*Akromesodon*) and *Mesodon* (*Mesodon*). Some of these convergences or parallelisms are confusing in the field. For example, specimens of *I. kalmianus* collected at GS-116, Knox County, Kentucky, initially were mistaken for *M. clausus*, with which they were microsympatric.

In addition, there are several convergent deviations from the general pattern of conchological stasis within subgenera. The most

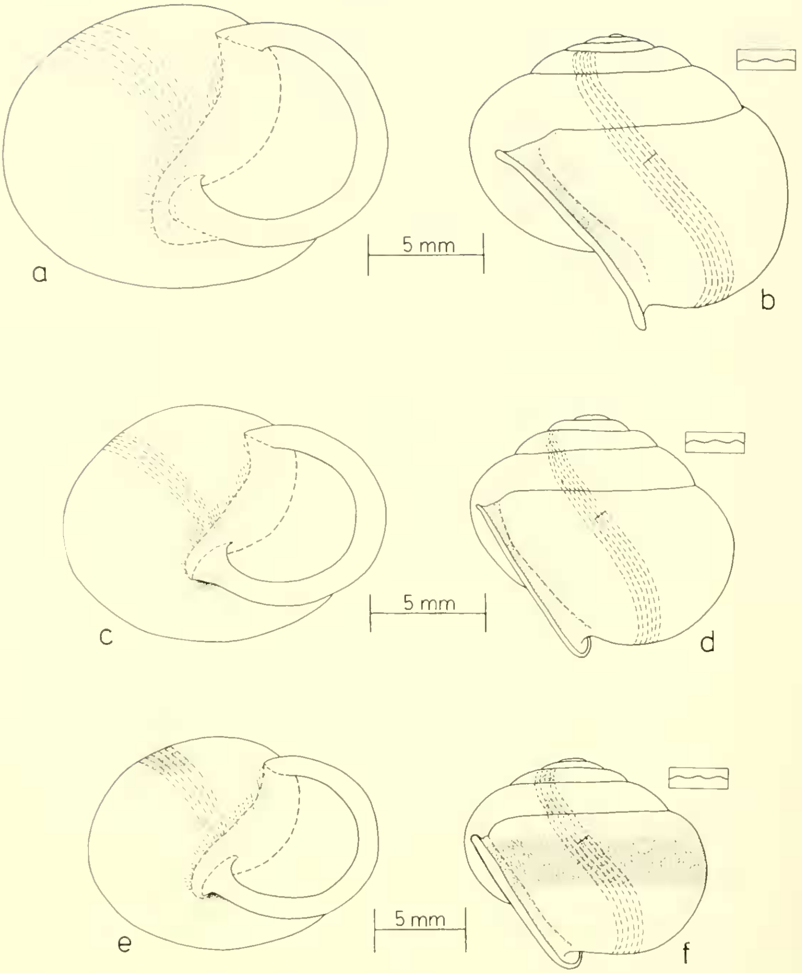


FIG. 37. Shells. a,b. *Mesodon mitchellianus,* Hubricht 19406 #A. c,d. *Mesodon clausus,* GS-116 #3. e,f. *Mesodon trossulus,* GS-53 #A.

striking of these is between *Patera* (*Patera*) *clarki* (Fig. 47c,d), which is an aberrantly high-spired member of its subgenus, and *Mesodon* (*Aphalogona*) *elevatus* (Fig. 38c,d), which differs from other members of its subgenus in having a long, basal lamella. *P. clarki* looks superficially like a miniature *M. elevatus,* but close examination reveals important differences in the relative size, shape and angle of the aperture.

Other shell convergences among subgenera are not so close. *Patera* (*Vesperpatera*) approaches *Mesodon* (*Mesodon*), but has more depressed spires and apertures (Fig. 52). *Mesodon* (*Appalachina*) has somewhat depressed spires, but has rounded apertures, very broad umbilici and coarse sculpture compared to the superficially similar *Patera* (*Vesperpatera*). The obviously unidentate *Fumonelix* (Figs. 40c,d, 41, 42c,d) somewhat resemble those species of *Inflectarius* (*Inflectarius*) in which the teeth on the apertural lip are effaced [*I. magazinensis* (Fig. 43c,d), *I. verus* (not individually figured) and *I. subpalliatus* (Fig. 44a,b)]. Another convergence of members of different subgenera, also not very close, is that of *Inflectarius smithi* (Fig. 40e,f), which in its parietal tooth and basal lamella (Fig. 40e) resembles members of *Patera* (*Patera*) (Figs. 46, 47, 48c,d), which lack the periostracal hairs of *I. smithi,* however.

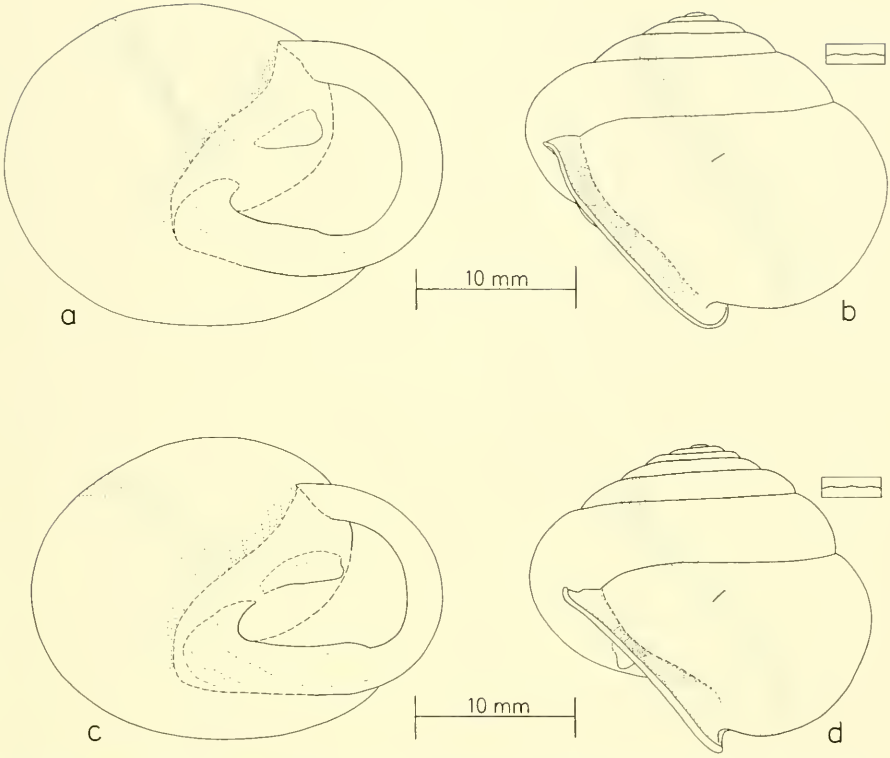


FIG. 38. Shells. a,b. *Mesodon zaletus,* GS-104 #21. c,d. *Mesodon elevatus,* GS-104 #33.

Further minor convergences occur among subgenera within a genus, such as the absence of periostracal hairs in both *I.* (*Hubrichtius*) (Figs. 35a,b, 45a,b) and *I.* (*Inflectarius*) (*I. ferrissi,* Fig. 44e,f). Within *Mesodon,* parietal teeth occur, seemingly independently, in *M.* (*Appalachina*) (*M. sayanus,* Fig. 39c), *M.* (*Aphalogona*) (*M. zaletus,* Fig. 38a; *M. elevatus,* Fig. 38c), and *M.* (*Mesodon*) (*M. thyroidus,* Fig. 36c); a reddish-brown color band occurs convergently in *M.* (*Aphalogona*) (some specimens of *M. elevatus:* Pilsbry, 1940: Fig. 440b), *M.* (*Akromesodon*) (some specimens of *M. altivagus:* Pilsbry, 1940: Fig. 437e), and *M.* (*Mesodon*) (*M. trossulus,* Fig. 37f); and an exposed umbilicus occurs in both *M.* (*Appalachina*) (Fig. 39a,c) and *M.* (*Mesodon*) (*M. clausus,* Fig. 36c; *M. thyroidus,* Fig. 37c). Within *Patera,* parietal teeth occur in both *P.* (*Vesperpatera*) (*P. roemeri*: Pilsbry, 1940: Fig. 449b,c; *P. leatherwoodi,* Fig. 49c,d) and *P.* (*Patera*) (Figs. 46, 47, 48c,d); and elevated spires occur in both *P.* (*Ragsdaleorbis*) (*P. pennsylvanica,* Fig. 45d) and *P.* (*Patera*) (*P. clarki,* Fig. 47d).

Within a subgenus, the pattern of distribution of a few minor shell characters among species is mosaic, with cases of convergence or parallelism. Within *Fumonelix,* periostracal hairs appear independently in *F. wetherbyi* and *F. wheatleyi* (subspecies *F. wheatleyi clingmanica* Pilsbry, 1904; Pilsbry, 1940: 736); and an enlarged shell with a reduced parietal tooth occurs in both *F. wheatleyi* (Fig. 42a,b) and *F. orestes* (Fig. 42e,f). Within *I. Inflectarius,* reduction or loss of teeth on the outer lip occurs in *I. magazinensis* (Fig. 43c), *I. verus* (not figured), *I. subpalliatus* and *I. ferrissi* (Fig. 44a,e).

DISCUSSION

Genitalic Analysis

As Pilsbry predicted (1940), penial sculpture proved a useful source of systematic characters in the Mesodontini. That it yielded fewer characters and character states than in

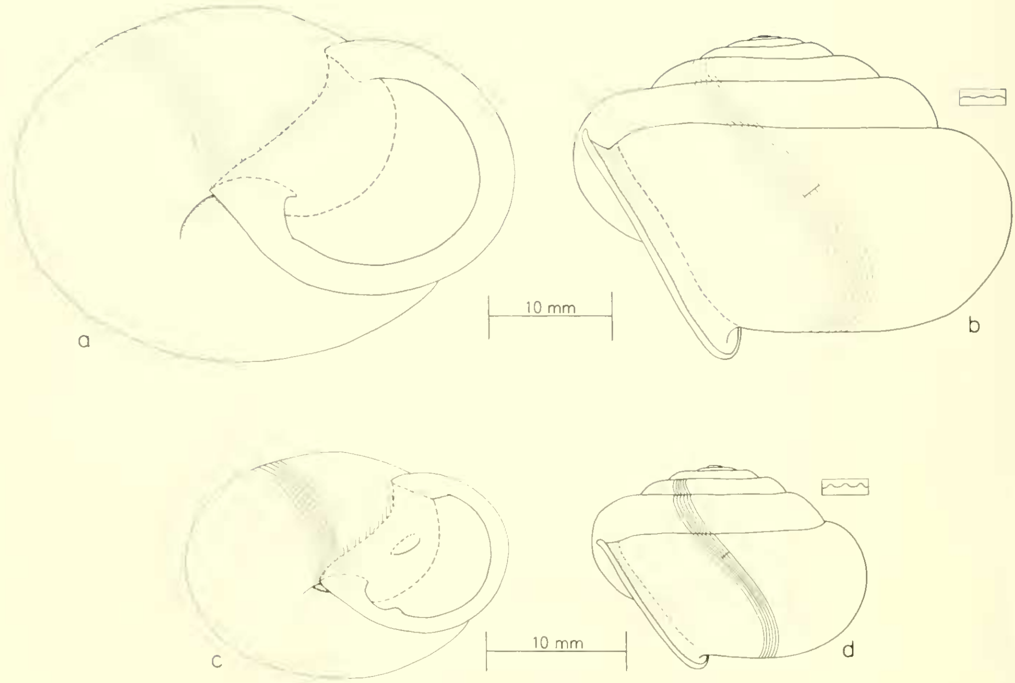


FIG. 39. Shells. a,b. *Mesodon chilhoweensis,* Hubricht 30943 #A. c,d. *Mesodon sayanus,* GS-130 #7.

the Triodopsini (Emberton, 1988) is hardly surprising. Because it is inserted during copulation, the triodopsin penis is subject in its morphology to many more forces of natural selection, including sexual selection, than is the mesodontin penis, which merely touches or intertwines with the mate's penis during copulation, but is never inserted (Fig. 1).

Owing to their plasticity and probable erectility, many of the penial structures in the Mesodontini sometimes are only tentatively interpretable. Investigation of variations among individuals and populations was essential to distinguishing real structures from preservational artifacts.

The suggested character-state transformations (Figs. 26–28) vary in plausibility. Characters might have been differently delineated, for example, the chalice might have been combined with the lateral pilasters, or each lateral pilaster treated entirely separately. The effect of such alternate approaches upon the outcome of phylogenetic analysis is unknown. Thorough documentation of the suggested character-state transformations provides objective, falsifiable hypotheses that might facilitate future, more enlightened revisions.

Allozymic Analysis

Starch-gel electrophoresis produces essentially one-dimensional characters: migration distances of stained bands on gels. Detection of convergences, whenever possible, depends on running the doubted alleles side-by-side, and preferably staggered, on the same gel. In this study, most suspected convergences were run on the same gel, but the magnitude of the project prevented side-by-side comparisons in many cases. Further, the large number of taxa and compared populations increased the probability of undetectable homoplasies.

Additional error is introduced by undetected alleles that indeed are possessed by a given species (Swofford & Olsen, 1990). Comparison of eight populations of *Mesodon zaletus* (Emberton, 1986), for example, showed two potential sources of undetected alleles in a species: low frequency and uneven geographical distribution. Both sources undoubtedly introduced a substantial number of spurious homoplasies into the allozymic data, resulting in low consistency indices for the cladograms (Table 5). The predictably high

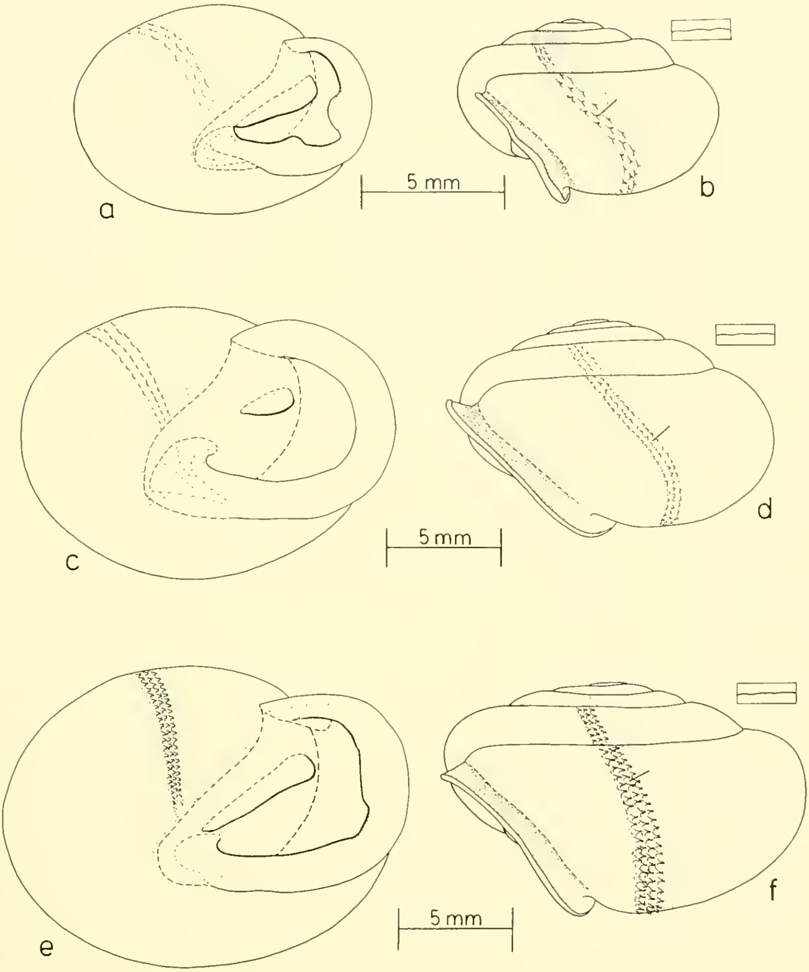


FIG. 40. Shells. a,b. *Inflectarius inflectus,* SC-130 #1. c,d. *Fumonelix wetherbyi,* GS-115 #4. e,f. *Inflectarius smithi,* GS-20 #1.

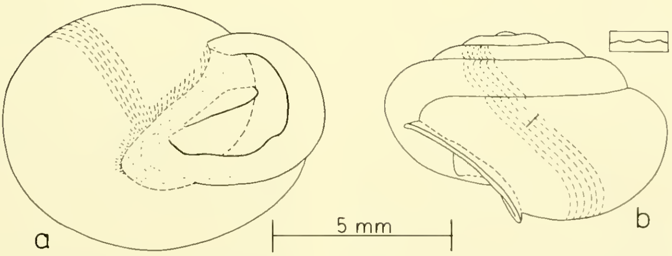


FIG. 41. Shell. a,b. *Fumonelix christyi,* GS-161 #10.

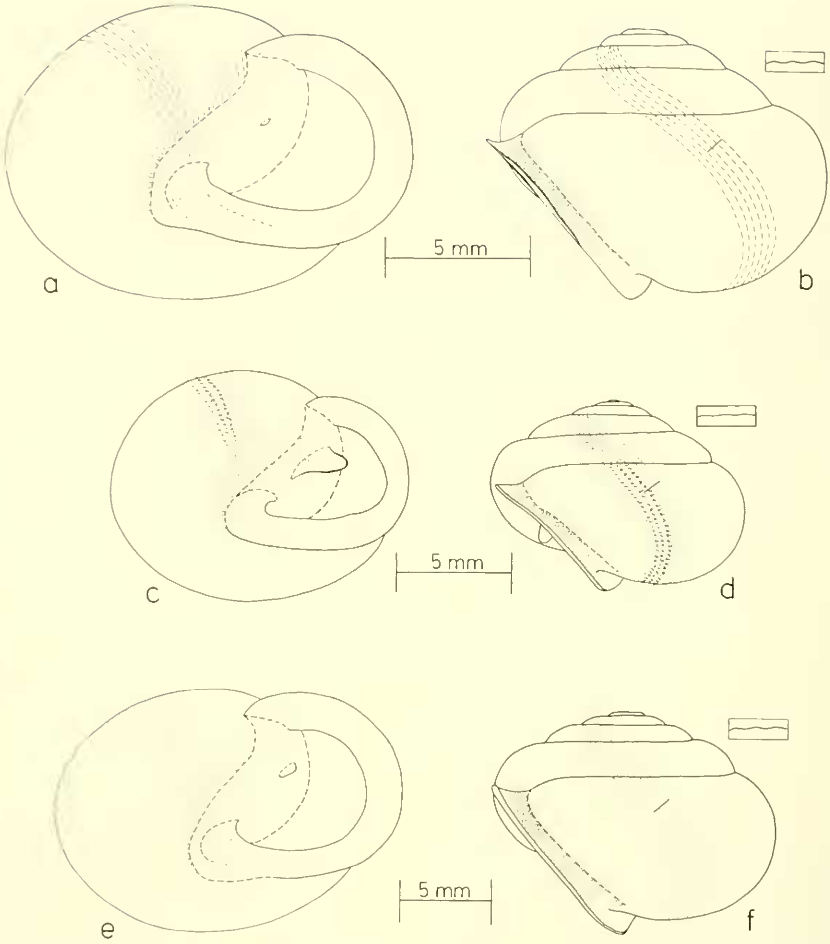


FIG. 42. Shells. a,b. *Fumonelix wheatleyi,* GS-6 #3. c,d. *Fumonelix jonesiana,* SC-155 #3. e,f. *Fumonelix orestes,* Hubricht 40465 #A.

incidence of real and false homoplasy in the allozymic data is offset, however, by the relatively large number of alleles that were detected. Thus, if all sources of error are random, the phylogenetic "signal" will be detectable through the "noise."

Phylogenetic Analysis

With the widespread use and acceptance of the maximum-parsimony method, and of the method of combining morphological with biochemical data for phylogenetic analysis, justification probably is not needed. In view of the controversy and flux in phylogenetic methodology, however, it seems worthwhile to document the reasoning behind the choices made in this study.

As systematists, we sample from a distribution of characters that have changed during the true phylogeny. Estimating the true phylogeny, then, is ideally a statistical problem, in which confidence limits can be placed upon each phylogenetic hypothesis based upon the size and distribution of samples, and upon inherent error of sampling (Felsenstein, 1983a, 1983b; Kim & Burgman, 1988). Realizing this ideal, however, depends upon having a probabilistic model of the evolutionary process (Felsenstein, 1982; Farris, 1983). The model commonly used for the statistical (maximum likelihood) approach to phylogenetic recon-

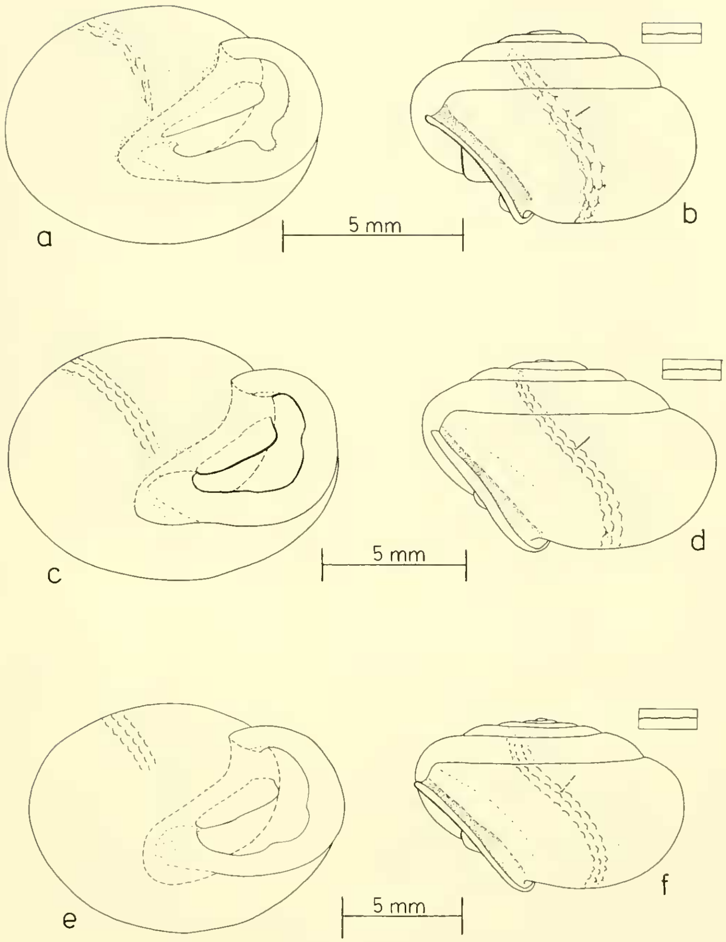


FIG. 43. Shells. a,b. *Inflectarius approximans,* Hubricht 23497 #A. c,d. *Inflectarius magazinensis,* GS-95 #17. e,f. *Inflectarius edentatus,* GS-90 #A.

struction based upon gene frequencies, introduced by Edwards & Cavalli-Sforza (1964), assumes that the arc-transformed frequencies are in Brownian motion on an infinite scale (Felsenstein, 1982; Rohlf & Wooten, 1988; Kim & Burgman, 1988). Although related random models of morphological change effectively mimic robust phylogenetic hypotheses from real data (D. M. Raup, pers. comm.), correlation does not imply causation. Such random models might be sufficiently accurate depictions, however, of evolutionary adaptations to effectively random climatic and biotic changes (L. Van Valen, pers. comm.).

If such models are accepted, then the most accurate and reliable method of phylogenetic estimation is maximum likelihood, using Felsenstein's (1986) CONTML program, part of his PHYLIP package (see Kim & Burgman, 1988). From the little that is known of the population biology and population genetics of polygyrid snails (McCracken, 1976; McCracken & Brussard, 1980; Emberton, 1986), there is not any reason to reject this model of evolution. The goal of this research, however, is to establish a phylogenetic framework for understanding the mechanisms of evolution in this group of snails. Until these mechanisms are understood, therefore, phylogenetic reconstruction should use methods devoid of assumptions about these mechanisms (Farris, 1983).

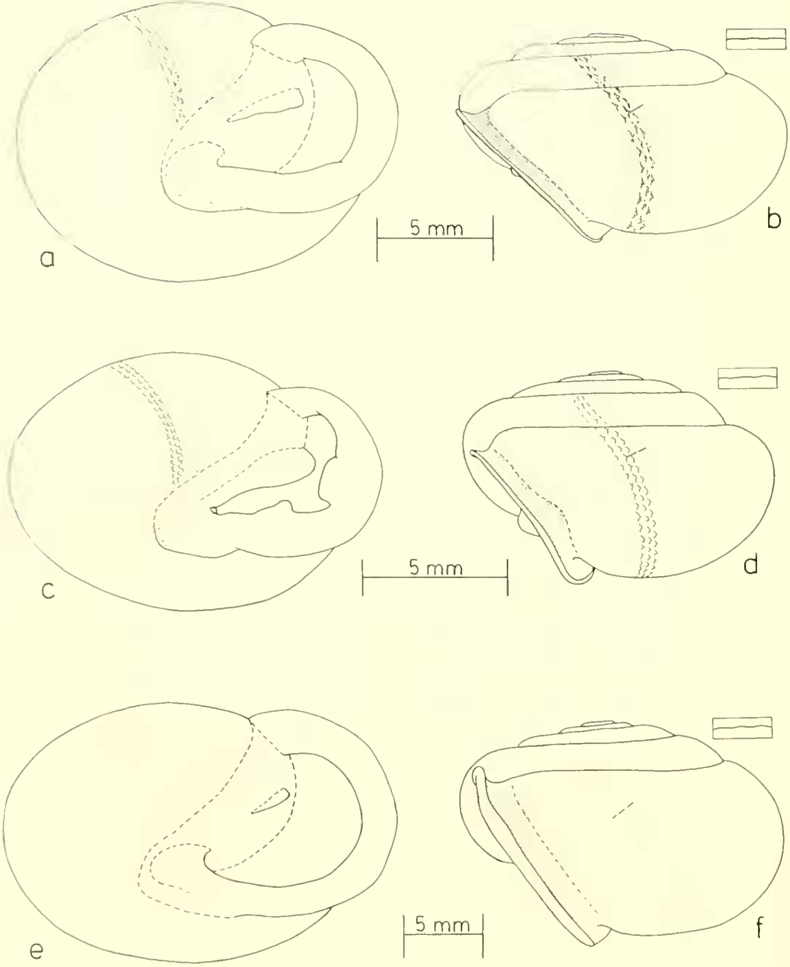


FIG. 44. Shells. a,b. *Inflectarius subpalliatus,* GS-153 #8. c,d. *Inflectarius rugeli*, GS-130 #8. e,f. *Inflectarius ferrissi*, SC-144 #A.

In the absence of probabilistic assumptions about the evolutionary process, the array of methods for phylogenetic reconstruction can be divided into those using the character data directly, and those that begin by reducing the data to distances among examined taxa. Not only is much critical information lost by condensing structured data into a single index, but all methods that use distance data (whether clustering or pairwise; Felsenstein, 1982) carry the sometimes, perhaps often, false assumption of equal rates of evolution (e.g. Farris, 1983). The effect of unequal rates of evolution on the ability of a distance method to detect a "true" simulated phylogeny can be alarmingly severe (Kim & Burgman, 1988). For these reasons, distance methods of phylogenetic reconstruction were not used in this study.

Non-distance, non-probabilistic methods all converge on Hennig's method (1966) whenever the data are completely free of undetected homoplasies (i.e., parallelisms, convergences and reversals). This traditional method, seemingly first codified by Mitchell (1901, cited in Nelson & Platnick, 1981) finds the shortest branching tree (cladogram) along which the taxa are connected by unique transitions between states (variants) of characters (homologous structures). Rarely is such a data set encountered, and characters are usually found to be incongruent. Whenever

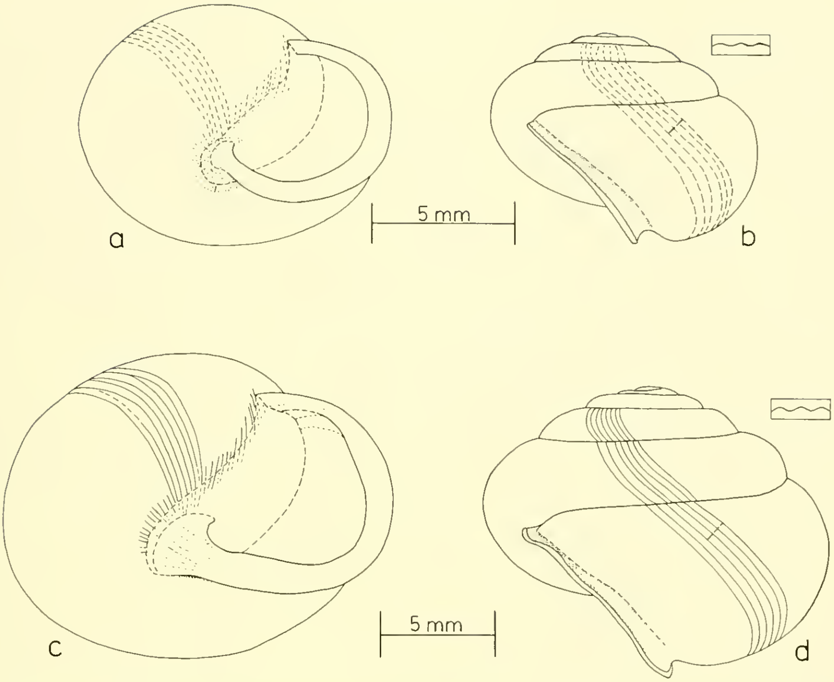


FIG. 45. Shells. a,b. *Inflectarius downieanus,* Hubricht 30825 #A. c,d. *Patera pennsylvanica,* SC-246 #1.

the characters are incongruent, and whenever careful reassessment fails to detect all homoplasies, then various algorithms having different biological assumptions can serve to reach a compromise solution to the conflicting data (Felsenstein, 1982).

None of these algorithms is free of risk, and all are most prone to error (as defined by inconsistency in the maximum-likelihood model; see Farris, 1983) whenever homoplasy is common and whenever evolutionary rates are markedly variable (e.g. Felsenstein, 1982; Rohlf & Wooten, 1988; Kim & Burgman, 1988). These algorithms comprise two categories: parsimony, which minimizes the number of homoplasies among all characters; and compatibility, which minimizes the number of characters having homoplasies (Felsenstein, 1982). Compatibility, or clique, analysis (Meachum, 1981; Le Quesne, 1982) suffers from the covering assumption that if a character shows some homoplasy, then all points of similarity in that character are homoplasies—otherwise phylogenetic information is discarded whenever a character is discarded because it shows homoplasy (Farris, 1983).

Methods of parsimony currently are divisible into those banning reversals (Camin-Sokal parsimony), those banning convergence and parallelism (Dollo parsimony), those lacking restrictions (Wagner parsimony), and those banning convergence and parallelism but permitting polymorphism (polymorphism parsimony) (Felsenstein, 1982). Given that specialists on stylommatophoran land snails universally accept the prevalence of morphological convergences (e.g. Solem, 1978; Emberton, 1988; Tillier, 1989), and that rather drastic morphological reversals are postulated for various groups of land snails (W. B. Miller, pers. comm.; Nordsieck, 1987; Emberton, 1986, 1988, in prep.), unrestricted parsimony is preferred. Of the plethora of available methods for phylogenetic reconstruction, therefore, Wagner unrestricted parsimony (Kluge & Farris, 1969; Farris, 1970) is the one used in this study.

An exact maximum-parsimony solution was technically not feasible for the large data matrix generated (Table 4). The heuristic method used (mhennig* bb* options of Hennig86: Farris, 1988) has been found in recent, extensive, empirical tests to arrive at cladograms as short as, or shorter than, those produced by any other algorithm (Platnick, 1989).

The importance of combining all available

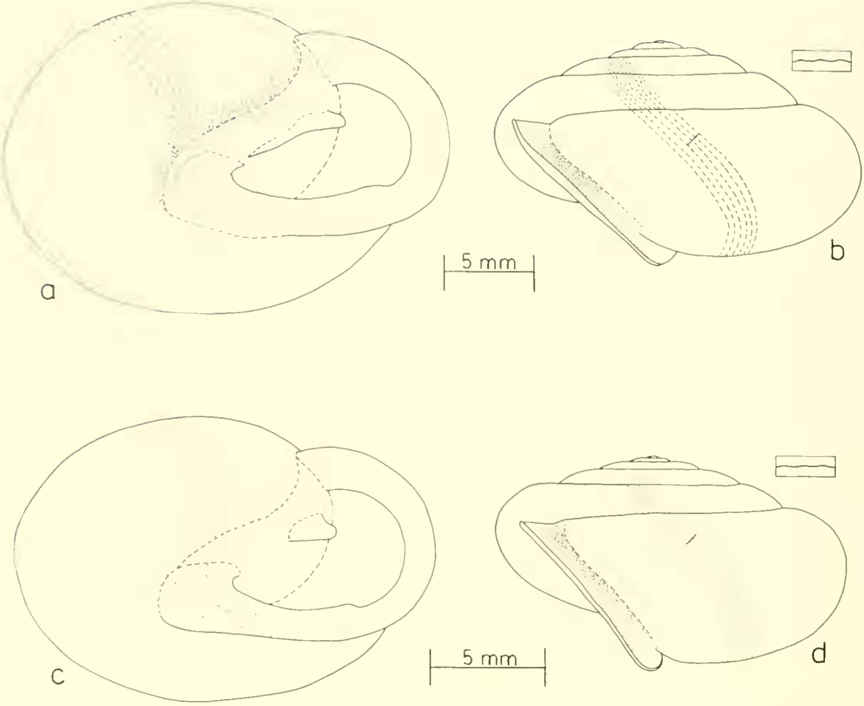


FIG. 46. Shells. a,b. *Patera panselana*, GS-142 #A c,d. *Patera perigrapta*, GS-98 #3.

data, both morphological and molecular, for phylogenetic analysis has been ably defended by Hillis (1987) and Kluge (1989), among others. Although one-dimensional allozymic data obviously should receive a lower weight than three-dimensional anatomical data, there is not any truly objective way to assign weights (see Emberton, 1988, and Appendix 3 for one attempt to solve this problem). The choice of assigning six different weights pursued in this study led to some very interesting results. This method has the advantage of refining detection of discrepancies between allozymic and genitalic data, thus allowing detection of misleading convergences in both data sets (for example, the convergent dorsal penial structures in *Patera appressa*).

A disadvantage of comparing the results of different and greater weightings of anatomical data with respect to allozymic data, however, is that the comparisons are tedious and subjective. An alternative approach is Farris's method (1988) of successive weighting. This method first produces a set of maximum-parsimony trees, assigns each character a weight (0–10) according to its degree of fit to these trees, reruns the analysis with the assigned weights, reweights each character in accordance with the resulting trees, and iterates this process until the character-weights stabilize. Although successive weighting "has the advantage of providing a means of basing groupings on more reliable characters without making prior decisions on weighting" (Farris, 1988), it has been rightly criticized for its inherent circularity (Swofford & Olsen, 1990: 499).

Application of successive weighting to the data set (Appendix 2) produces the strict consensus tree shown in Figure 53. This tree wholly supports that shown in Figure 52 in its phylogenies of *Mesodon* and *Fumonelix*, which therefore can be considered robust with respect to methodology. The resolution of the tree in Figure 53 is less for the other two genera, however, and there are some differences from Figure 52. The most important difference is in placing the pair *I. subpalliatus* and *I. ferrissi* as sister group to the pair *I. inflectus* and *I. rugeli*, rather than at the base of a larger clade including these two species. This solution is exactly that obtained in alternative analyses of the some of the same data (Emberton, 1986, in press; Appendix 3), and

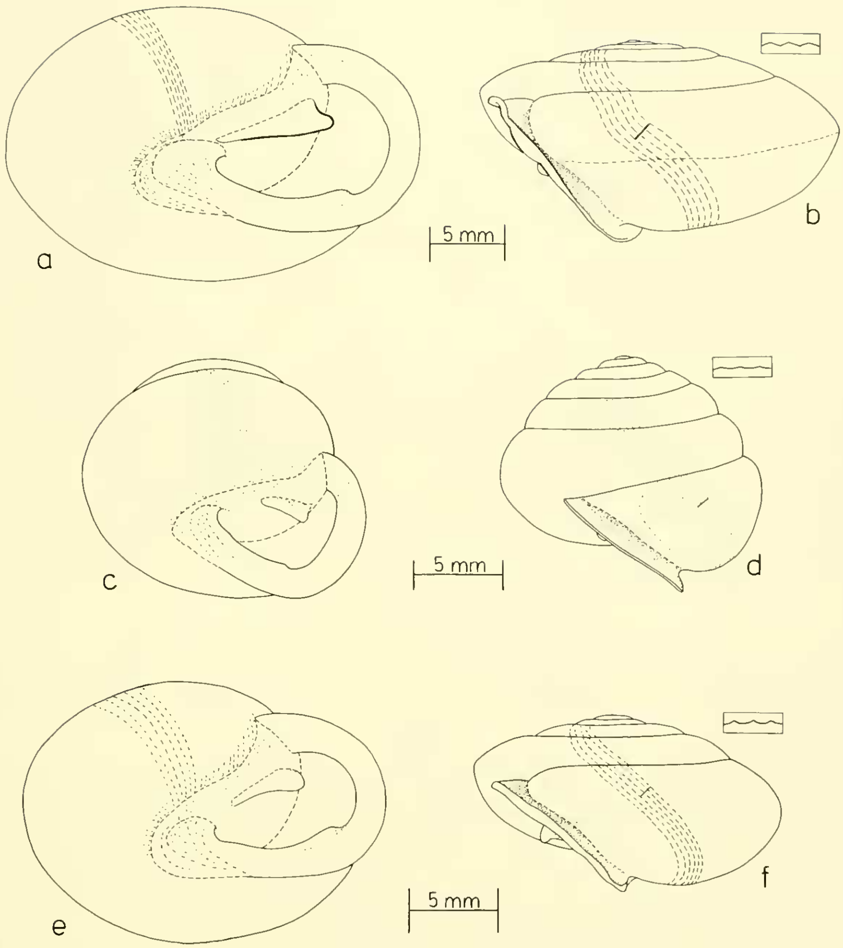


FIG. 47. Shells. a,b. *Patera sargentiana*, GS-101 #2. c,d. *Patera clarki*, GS-1 #3. e,f. *Patera appressa*, GS-104 #2.

thus is a more robust hypothesis for evolution within *Inflectarius*.

Separate analyses of genitalic and allozymic data, with construction of a consensus from weighted trees (Appendix 3), results in a topology (Fig. 60) very similar to that produced by the preferred method (Fig. 52, Appendix 1). This alternative and rather complicated analysis (procedure outlined in Figure 54) shows a high degree of congruence between anatomical and electrophoretic data sets. Its resulting consensus differs most significantly in the placements of the *Inflectarius ferrissi-subpalliatus* clade (mentioned above) and of *Mesodon* (*Appalachina*), which admittedly is considered tentative in Figure 60.

In sum, two alternative phylogenetic analyses, one of them quite different in approach and even in its outgroup, support to a high degree that shown in Figure 52.

Revised Classification

The revised classification (Appendix 1) follows the phylogenetic hypothesis depicted in Figure 52. Within the limits of accuracy of the data, the phylogenetic hypotheses concerning *Fumonelix* and *Mesodon* can be considered fairly robust, as noted above. Thus the classifications and inferred phylogenies of *Fumonelix* and *Mesodon* are based entirely upon genitalic and allozymic data. For the more plesiomorphic genera, *Patera* and *Inflectarius*, these data are less conclusive, and

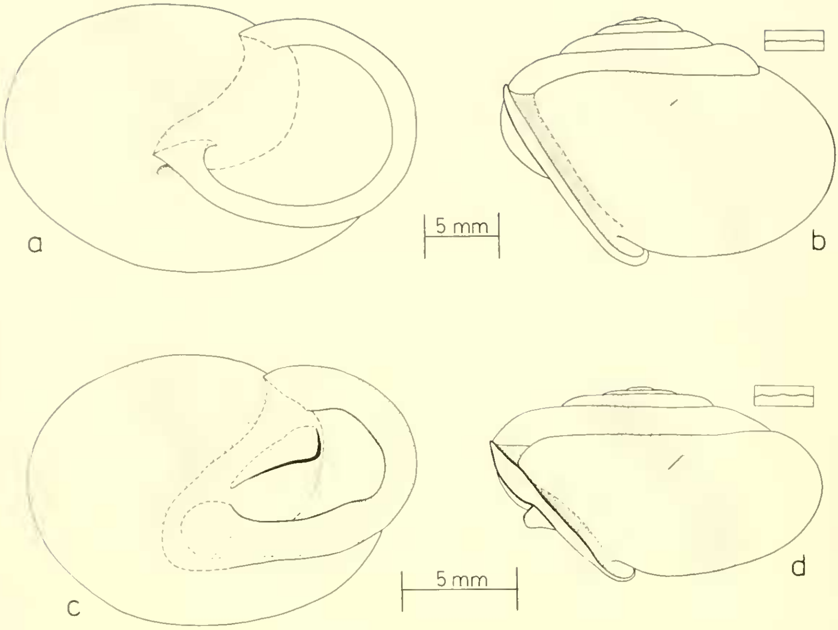


FIG. 48. Shells. a,b. *Patera binneyana* "long", FMNH 176008 #B. c,d. *Patera laevior*, H-22 #3.

hence more reliance is placed on shell morphology for the final classification.

Genitalic Evolution

Genitalic and geographic comparisons between 29 pairs of sister taxa (Table 7) detected evolutionary trends similar to those previously found in the Triodopsini (Emberton, 1988): sister taxa with peripatric geographical ranges usually show little or no difference in penial sculpture; those with sympatric ranges show only moderate differences; and all examples of great genitalic differences, and most examples of moderate genitalic differences, occur between sister taxa with parapatric or allopatric ranges. The caveats about interpreting these results were discussed by Emberton (1988: 236).

In addition, population-level comparisons for 16 species (Table 7) failed to find any trace of character displacement in penial morphology.

These findings support and generalize the hypotheses made for the Triodopsini (Emberton, 1988) that (1) peripheral isolates generally do not differentiate, (2) differentiation due to reproductive character displacement is moderate at most, and (3) major differentiation is rare, rapid, and occurs in isolates; they do not support the hypothesis that vicariant isolates generally differentiate slowly. Full discussion of these hypotheses and their implications appear in Emberton (1988). It is surprising to find so much similarity in patterns of genitalic evolution between the Mesodontini and the Triodopsini, despite the very different ways the penis functions during copulation in these two tribes (Webb, 1961, 1974; Emberton, 1986).

An important aspect of genitalic evolution in the Mesodontini is that a plesiomorphic or near-plesiomorphic morphology (lateral pilasters simple, chalice a simple continuation of the lateral pilasters, other sculpture absent) occurs in three of the four genera, including the most apomorphic genus (Fig. 52). Thus, although it is characteristic of *Patera*, this morphology also persists in *Inflectarius* (*I. kalmianus*, Fig. 11a; *I. edentatus*, Fig. 12c; *I. verus*, Fig. 14) and, surprisingly, with little modification in *Mesodon* (*Appalachina*) (Fig. 18). Such conservatism—or atavism, by another interpretation—was not found in the genitalic evolution of the Triodopsini (Emberton, 1988).

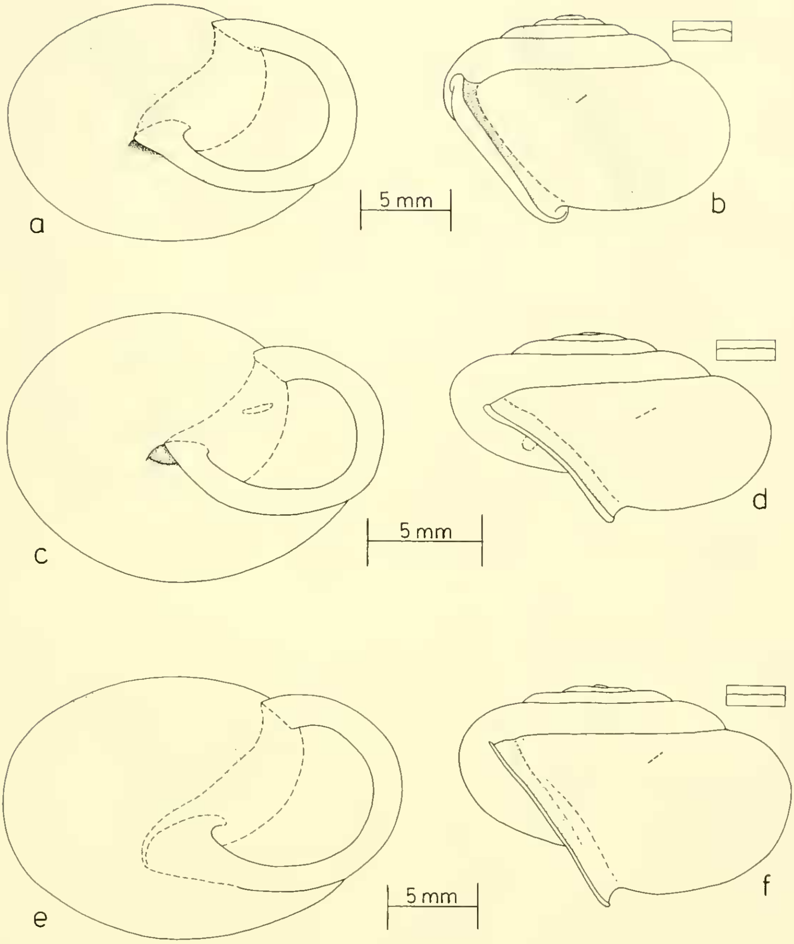


FIG. 49. Shells. a,b. *Patera binneyana* "short", Hubricht 31615 #A. c,d. *Patera leatherwoodi,* GS-67 #1. e,f. *Patera roemeri,* GS-63 #4.

Shell Evolution

With important and striking exceptions, each genus has features characteristic of its shell morphology. *Patera* shells are generally medium-sized, smooth and depressed; *Inflectarius* shells are typically small, hirsute and tridentate; those of *Fumonelix* tend to be small, smooth and unidentate; and *Mesodon* shells are usually large, smooth and globose.

Each subgenus of the Mesodontini is relatively fixed, or evolutionarily static, in its shell morphology. Exceptions are rare and either unique [the high spire of *Patera* (*Patera*) *clarki*] or parallel [reduction or loss of apertural tooth in *Inflectarius* (*Inflectarius*) *ferrissi,* and, to a lesser extent, in some other members of this subgenus, and in *Fumonelix wheatleyi, F. orestes* and *Mesodon* (*Aphalogona*) *mitchellianus*].

Some of the subgenera with static shell morphologies are conchologically similar. The most conspicuous example of this similarity is the globose, toothless, imperforate, hairless shell morphology that occurs in at least one subgenus of all four genera (Fig. 52). According to the phylogenetic hypothesis, this sort of shell is plesiomorphic in the two most plesiomorphic genera (*Patera* and *Inflectarius*), and also occurs among the proposed close outgroups of the Mesodontini (Fig. 52). It is reasonable to hypothesize, therefore, that this

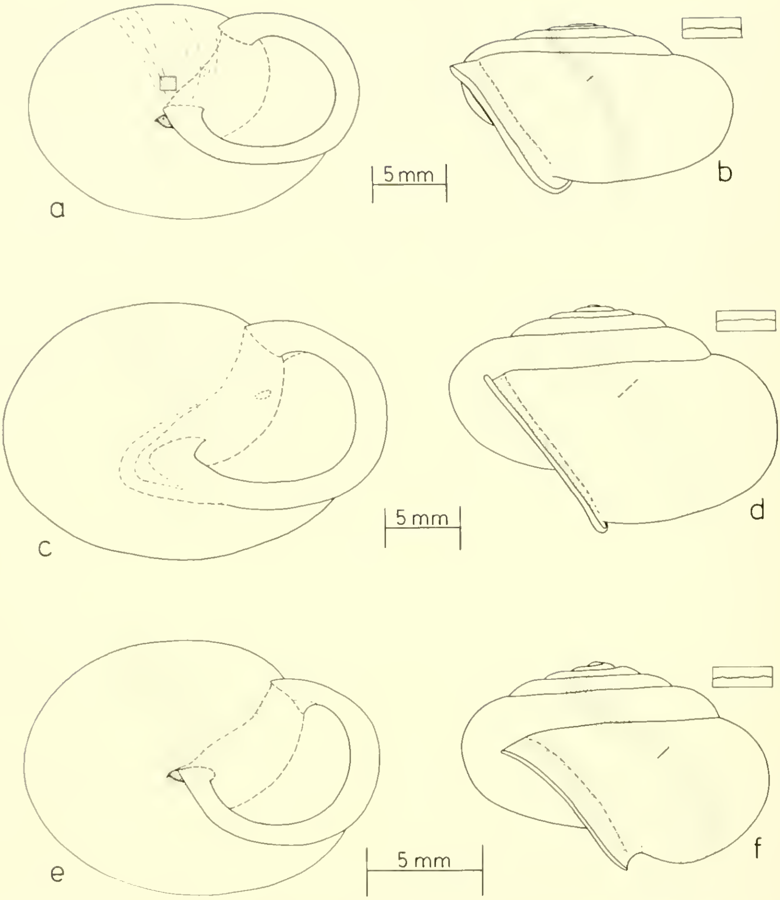
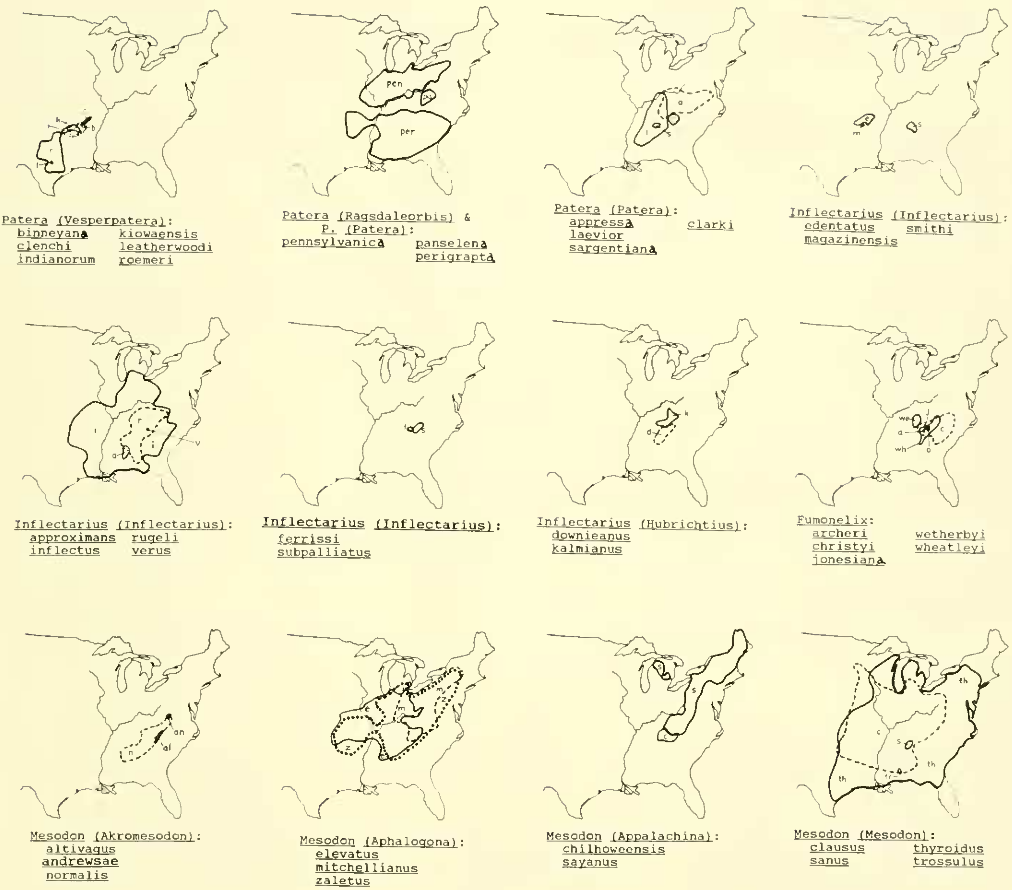


FIG. 50. Shells. a,b. *Patera clenchi*, Hubricht 25210 #A. c,d. *Patera roemeri*. e,f. *Patera kiowaensis*, GS-84 #7.

shell form is plesiomorphic within the Mesodontini.

If this hypothesis—that the common ancestor of the Mesodontini had a globose, toothless, imperforate, hairless shell—is correct, then several parallelisms among genera follow from an acceptance of the phylogenetic hypothesis (Fig. 52). First, a parietal tooth has evolved separately at least once within each of the four genera. Second, a basal lamella has evolved at least three times [in *P.* (*Patera*), in *I.* (*Inflectarius*) *smithi* and in *Mesodon* (*Aphalogona*) *elevatus*]. Third, an exposed umbilicus has evolved three times [in *Patera* (*Vesperpatera*), in *Mesodon* (*Appalachina*) and in *M.* (*Mesodon*)]. Fourth, periostracal hairs have evolved at least twice [in *I.* (*Inflectarius*) and in *Fumonelix*], and more probably three times, because the hairs of *F. wetherbyi* and *F. wheatleyi clingmanica* seem to be inhomologous.

One can only speculate about the presumed adaptive values of these parallel structures. Apertural teeth, or denticles, have been interpreted as barriers against insect predators (review in Goodfriend, 1986; Emberton, 1988), but without substantial experimental evidence. Some of the parietal teeth in the Mesodontini are rather small and only slightly obstruct the entire aperture, although they might substantially obstruct the open pneumostome. An alternative, or auxiliary, hypothesis is that a parietal tooth directs body wastes away from the body of the animal during crawling. The basal lamina must strengthen the lower lip of the aperture, a fea-



Patera (Vesperpatera):
binneyana kiowaensis
clenchi leatherwoodi
indianorum roemeri

Patera (Ragsdaleorbis) &
P. (Patera):
pennsylvanica panselena
perigrapta

Patera (Patera):
appressa clarki
laevior
sargentiana

Inflectarius (Inflectarius):
edentatus smithi
magazinensis

Inflectarius (Inflectarius):
approximans rugeli
inflectus verus

Inflectarius (Inflectarius):
ferrissi
subpalliatus

Inflectarius (Hubrichtius):
downieanus
kalmianus

Fumonelix:
archeri wetherbyi
christyi wheatleyi
jonesiana

Mesodon (Akromesodon):
altivagus
andrewsae
normalis

Mesodon (Aphalogona):
elevatus
mitchellianus
zaletus

Mesodon (Appalachina):
chilhoweensis
sayanus

Mesodon (Mesodon):
clausus thyroidus
sanus trossulus

FIG. 51. Range maps of 42 species of Mesodontini, arranged by revised subgenera. Adapted from Hubricht (1985).

ture of benefit to cliff-dwelling species such as *P.* (*Patera*) *laevior* as they drag their shells into narrow crevices in the rock; the majority of mesodontin species with basal laminae are not cliff-dwellers, or even talus-dwellers, however (Emberton, 1986). The benefit, if any, of an exposed umbilicus is unknown. No mesodontin is known to brood its eggs in its umbilicus, nor does the umbilicus of litter-dwelling species seem to have the disadvantage of accumulating debris, although known burrowing species such as *Fumonelix archeri* (W. & A. Van Devender, pers. comm.) are imperforate. Periostracal hairs presumably either protect the shell from contact with acidic, decaying leaves, or accumulate soil and debris that camouflage the shell from visual or tactile predators, or both. Although these conchological characters seem to be adaptive because of their parallel derivations, their functions are unknown; hypotheses are at least available for testing. Unfortunately, not enough is yet known about the detailed ecology of these animals to test the hypotheses (see Emberton, in press).

Recommendations for Future Research

Several systematic problems in the Mesodontini remain unresolved. First, the monophyly of this tribe is still in question; the plesiomorphic penial morphology occurs in various outgroups (Fig. 52), and no unequivocal synapomorphy phylogenetically unites the Mesodontini. Second, the true phylogenetic position of the aberrant *Patera pennsyl-*

TABLE 7. Comparison of difference in penial morphology with relationship between geographic ranges for 29 pairs of sister taxa of the Mesodontini according to the phylogeny in Figure 52. Taxa are designated by abbreviations used in Table 4. * = substantial difference in length only.

Phylogenetically Adjacent Taxa	Penial Shift	Geographical Relationship
rugel vs. apprx	great	parapatric
subpl vs. ferrs	great	parapatric
wethr vs. wheat group	great	allopatric
norml. vs. altiv	great	parapatric (?)
penns vs. rest of Patera	moderate	parapatric
perig vs. pansl	moderate*	allopatric
apprs vs. laevr	moderate	parapatric (?)
apprs vs. sargt	moderate	allopatric
downi vs. kalmn (?)	moderate	parapatric
edent vs. magaz	moderate	peripatric
edent vs. smith	moderate	allopatric
magaz vs. smith	moderate	allopatric
inflc vs. rugel	moderate	sympatric
inflc vs. apprx	moderate	peripatric
chrst vs. rest of Fumonelix—wethr	moderate	sympatric (?)
sayan vs. chilh	moderate*	parapatric
zalet vs. mitch	moderate	sympatric
roemr vs. leath	slight	peripatric
laevr vs. sargt	slight	peripatric (?)
binny group vs. apprs group—apprs	slight	allopatric
wheat group (4 spp. *inter se*)	slight	allo- or peripatric
elevt vs. zalet	slight	sympatric
andrw vs. norml	slight	peripatric
thyrd vs. claus	slight	sympatric
thyrd vs. tross	slight	peripatric
binny subgroup vs. clench subgroup	none	sympatric
perig subgroup vs. clark	none	peripatric
sanus vs. rest of thyrd group	none	peripatric
claus vs. tross	none	peripatric (?)

vanica is unclear, whether is it a member of a monophyletic *Patera* clade, or a relict or unique member of an isolated, plesiomorphic genus within or without the Mesodontini. Third, the status of *P. leatherwoodi* as a separate species, rather than as a small relict population of *P. roemeri*, needs to be determined. Fourth, it is unclear whether the two genitalic forms of *P. binneyana* are separate species, or extremes of a continuum between populations with long and with short penes. In either case, the evolutionary mechanism by which extremely long penes evolve in land snails (Figs. 23, 24; Solem, 1974: fig. 12) remains to be determined, although presumably it involves runaway sexual selection (Fisher, 1930), a phenomenon poorly understood in hermaphrodites. Fifth, it is not clear whether the morphologically similar and geographically parapatric *P. perigrapta* and *P. panselena* constitute one or two true species. Sixth, the systematic status of the several geographic forms of *P. clarki* remain incompletely assessed; for example, it is unknown whether the endangered *P. clarki nantahalae* is a species, a subspecies, or an ecophenotypic variant. Seventh, the phylogenetic placement of *Inflectarius downieanus* needs to be tested with both relaxed anatomical material and with allozymic analysis. Because of their important evolutionary implications, the plesiomorphic positions of *I. kalmianus* and *I. downieanus* within *Inflectarius* (Fig. 52) should be tested using additional data sets. Eighth, the species status of *I. verus* needs testing, in part to determine whether Hubricht (1985) was correct in synonymizing it with *I. subpalliatus*. Ninth, more data are needed to allow better zoogeographic analyses of *Patera* and *Inflectarius*. The phylogenetic relationships among the Ozarkian and Appalachian members of both of these genera (Fig. 51) need more robust hypotheses (compare Figures 53, 54). Tenth, relationships within the terminal taxa of *Fumonelix* require further investigation, using more characters and more

TABLE 8. Localities (state:county) of populations dissected in searches for reproductive character displacement between pairs of conchologically similar species of the Mesodontini. Number of specimens dissected from each population in parentheses. TX = Texas, AL = Alabama, AR = Arkansas, TN = Tennessee, KY = Kentucky, NC = North Carolina, IN = Indiana.

Species A	Allopatry	Sympatry	Allopatry	Species B
roemeri	TX:Travis (1)	TX:Bastrop (5,5)	TX:Cherokee (3)	*thyroidus bucculentus*
inflectus	AL:Madison (1) TN:Blount (3) KY:Henderson (3)	AR:Logan (1,3)	—	*magazinensis*
inflectus	AL:Madison (1) KY:Henderson (3) AR:Logan (1)	TN:Blount (3,3)	NC:Swain (3)	*rugeli*
wheatleyi	NC:Avery (3)	NC:Haywood (3,1)	NC:Swain (3)	*clarki*
zaletus	TN:Blount (1) AR:Crawford (1) NC:Swain (1)	TN:Franklin (5) IN:Owen (3)	—	*elevatus*
zaletus	TN:Blount (1) AR:Crawford (1) TN:Franklin (5) IN:Owen (3)	NC:Swain (1,1) TN:Cocke (0,3)	NC:Macon (3) NC:Macon (2)	*normalis*
zaletus	TN:Blount (1) AR:Crawford (1) TN:Franklin (5) IN:Owen (3)	NC:Swain (1,1)	NC:Swain (2)	*altivagus*
normalis	NC:Macon (3) NC:Macon (2)	NC:Swain (1,1)	NC:Swain (2)	*altivagus*
normalis	NC:Swain (1) NC:Macon (2) TN:Blount (3)	NC:Macon (3)	—	*thyroidus*
clausus	TN:Blount (4)	KY:Knox (3)	—	*kalmianus*

populations. Preliminary studies (F. G. Thompson, unpublished; Emberton, unpublished) indicate complex and sometimes intergrading variations in both shell and genital morphologies in the species of the Smoky Mountain and those of adjacent areas. This radiation is fascinating and poorly understood. Further, because of their highly aberrant shell form and plesiomorphic genitalia, *Mesodon sayanus* and *M. chilhoweensis* should be more thoroughly investigated to test their current phylogenetic placement. Again, the position of *M. mitchellianus* within *M.* (*Aphalogona*) is likewise suspect. Further, the limits and relationships of species within *M.* (*Akromesodon*) remain problematic. For example, it is unclear whether *M. altivagus* is truly separate from *M. andrewsae.* This entire complex, like *Fumonelix,* is a variable and incompletely understood component of the land-snail fauna of the Southern Appalachians. Finally, whether *M. trossulus* is truly separate from *M. clausus* or part of a local polymorphism is unclear.

The Mesodontini, because of their species diversity, their phylogenetic hypothesis, their mapped ranges of species, and their broad conchological, genitalic and allozymic variation, are an excellent system for further evolutionary studies. For example, the three widespread clades (*Patera, Inflectarius* and *Mesodon*) could be compared as to their modes of speciation; their covariations among the evolutionary rates of anatomy, shell and allozymes; their phylogenetic changes in ontogeny of the shell, as measured from sections or X-radiographs of adult shells (Raup, 1966); their rates of spread from Pleistocene refugia as determined from geographic variation of allozymes; and their evolutionary and phenotypic plasticities of shell shape.

A most promising aspect of the Mesodontini for the study of evolution is the fact that

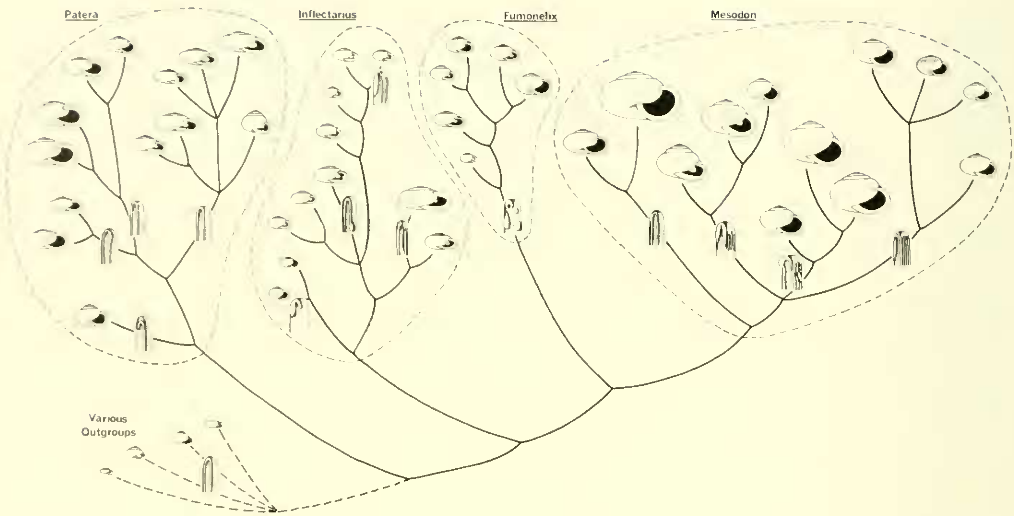


FIG. 52. Evolution of shell morphology and upper penial sculpture in the Mesodontini. The ten clades designated as subgenera are (from left to right) *Patera* (*Ragsdaleorbis*), *P.* (*Vesperpatera*), *P.* (*Patera*), *Inflectarius* (*Hubrichtius*), *I.* (*Inflectarius*), *Fumonelix, Mesodon* (*Appalachina*), *M.* (*Aphalogona*), *M.* (*Akromesodon*), and *M.* (*Mesodon*).

their conchological radiation has been iterated by the distantly related, confamilial tribe Triodopsini (Pilsbry, 1940; Emberton, 1988). These two tribes have very nearly the same geography, ecology, conchology and species richness (Emberton, 1986, 1988). This monograph on the Mesodontini complements that on the Triodopsini (Emberton, 1988) in laying the phylogenetic basis for using these convergent, sympatric radiations to address general questions about the evolutionary morphology of gastropod shells.

ACKNOWLEDGMENTS

This paper is adapted from part of a doctoral dissertation approved by the Committee on Evolutionary Biology, University of Chicago. I am grateful to my advisor, the late Alan Solem, to whose memory this paper is dedicated, and to the members of my proposal and defense committees: David Raup, Michael Wade, Bradley Shaffer, Russell Lande, Lynn Throckmorton, James Teeri and Harold Voris. For physical, moral, and secretarial support throughout this project, I am most grateful to Ellen Emberton.

This paper is a contribution of the Molecular Genetics Laboratory of the Department of Malacology, Academy of Natural Sciences of Philadelphia (ANSP). George Davis, Thomas Uzzell, Caryl Hesterman, John Hendrickson, Andrea Garback and Arthur Bogan were extremely helpful and encouraging hosts during my electrophoretic stints at the Academy.

For the loan of specimens under their care I thank the late Alan Solem, Field Museum of Natural History; George Davis, ANSP; and Leslie Hubricht, of Meridian, Mississippi. I also wish to thank Mr. Hubricht for generously providing then-unpublished range maps (Hubricht, 1985), precise locality data for several rare species, identifications of difficult material and advice for collecting.

For carrying much of the burden of labelling and cataloging my collections into FMNH, I am indebted to Margaret Baker, Patricia Johnson and Lucy Lyon.

For assistance in the field, I thank Ellen Emberton, Lucia Emberton, Ned Walker, Gene Bryant, Tony Bryant, Eugene Keferl, Leslie Hubricht, John Ahrens, John Petranka, Betsey Kirkpatrick, Glenn Webb, Wayne Van Devender, Amy Van Devender, Martha Van Devender, Wayne Evans, Arthur Bogan, Robert Lawton, John Pinkerton, Mark Southerland, Dennis Herman, Greg Mueller, Kisa Nishikawa, Phil Service, Joe Bernardo, Ken Baker, Alan Lo, David Kasmer and Brad Foster. Thanks also go to the many park rangers and property owners who permitted me to collect on their land, as well as to the many people who provided camping sites and other hospitality.

Glenn Webb generously shared his vast knowledge of the Polygyridae and allowed me to study his slide-mounted voucher specimens. He also graciously provided the live specimens of *Ashmunella.*

John Hendrickson (ANSP) has my very great gratitude for running most of the computer analyses of Appendix 3.

This paper benefitted greatly from the comments of George Davis, Carol C. Jones, and two anonymous reviewers. All errors are my own.

This work was funded by the following grants to the author: NSF Postdoctoral Fellowship BSR-87-00198; NIH Genetics Training Grant GM07197-07; Jessup Fellowship, ANSP; Bequaert Award, American Malacological Union; Hinds Fund, University of Chicago (UC); Research Grant, Highlands Biological Station, Highlands, North Carolina; Louer Fund, FMNH; Field-Collection Grant, Division of Invertebrates, FMNH; and Student Computation Fund, UC. Additional funding was also provided by an NIH grant to George M. Davis, and a USDA grant to Michael J. Wade.

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Revised Ms. accepted 26 December 1990

APPENDIX 1. SYSTEMATIC REVIEW FAMILY POLYGYRIDAE PILSBRY, 1894a SUBFAMILY POLYGYRINAE PILSBRY, 1894a

Tribe Mesodontini, Tryon

(Figs. 1-25, 35-50, 51; Table 2; Fig. 52)

Description

Genitalia: **upper penis** (apical, sculptured region of penis in the Triodopsinae and the

Ashmunellinae) **entirely absent;** sperm exchanged externally by deposition on mate's everted basal penis; basal penis (i.e., the entire penis) with **two longitudinal, lateral pilasters;** penis short to extremely long; lateral pilasters thin and varying from simple and uniform in length to unilaterally absent or thickened or extremely high and thin and to entirely absent; dorsal surface sometimes bearing an accessory pilaster, a system of thin to thick ridges, or one or more large bulges; **apical penis bearing a basin-like chalice,** varying from thin- to thick-walled, flexible to rigid, symmetric to asymmetric, continuous to discontinuous with lateral pilasters, and uneverted (a basin or scoop) to everted (a glans) whenever functional; **no penial sheath; penial retractor muscle attached to apex of penis; wall of spermathecal duct thin; no appendages, diverticulae or glands associated with genitalia.**

Shell: diameter 8 to 40 mm; widely umbilicate to imperforate; high globose-conic to lenticular; sculpture smooth to matte or coarsely ribbed or hirsute; parietal barrier absent, or present as a simple straight to slightly curved tooth; basal barrier absent, a simple tooth, a long lamella, or a baso-columellar peg; palatal tooth absent or a simple tooth.

Genus *Patera* Albers, 1850
(Figs. 10, 19-25, 45-50; Table 2; Fig. 52)

Type species: *Helix appressa* Say, 1821
Etymology: Latin "patera" (saucer).
Gender: feminine.
Description

Genitalia: left lateral pilaster variable; right lateral pilaster variable; **chalice generally a simple hood,** sometimes spatulate (right wall high and rounded, left wall inconspicuous) or seated atop barrel-shaped pedestal; **dorsal structures usually absent** (only type species has dorsal structures: thin, subparallel anastomosing cords); ventral structures absent; peripheral structures absent.

Shell: size **medium** (diameter 13-26 mm); shape **usually depressed** (height/diameter, 0.4-0.6), rarely globose (height/diameter, 0.7-0.8); umbilicus narrow and broadly covered, chinked or open; parietal denticle absent, slight or pronounced and blade-like; basal denticle absent or present as long, thin lamella truncated palatally; palatal denticle absent; **periostracal hairs or scales absent.**

Comparisons

Shell: *Patera* comprises all the Mesodontini with flat, hairless shells. West of the Mississippi, there are no other Mesodontini with which they could be confused, although they closely resemble several species of *Neohelix* (Polygyridae: Triodopsinae), one species of which, *N. lioderma* Pilsbry, 1902, was originally described as a subspecies of *Patera indianorum*. East of the Mississippi, all *Patera* shells have a characteristic blade-like parietal tooth and a long basal lamella; these features, together with a flat shape, make them confusingly convergent on the triodopsine genus *Xolotrema* Rafinesque, 1819 (see Emberton, 1988), with which they are sometimes sympatric. These shell characters easily distinguish from other Mesodontini all species of *Patera* with the exceptions of *P. perigrapta,* which sometimes has a fairly elevated spire, and *P. clarki,* which is aberrantly domical. These two species can resemble some hairless, large-toothed members of *Fumonelix,* particularly *F. archeri* and some specimens of *F. wheatleyi; Patera clarki* is also convergent on *Mesodon elevatus,* which is always at least twice as large and much more heavily calcified. *Patera* shells are never hirsute—i.e., they lack hair-like or scale-like periostracal processes—a feature that readily separates them from several species with somewhat convergent shell shapes: *Inflectarius smithi, I. verus, I. subpalliatus, Fumonelix wetherbyi* and *F. jonesiana.*

Subgenus *Ragsdaleorbis* Webb, 1954b
(Figs. 10b, 45c,d; Table 2; Fig. 52)

Type species: *Helix pennsylvanicus* Green, 1827, by original designation.
Etymology: Ragsdale (John P. Ragsdale, Jr., of Indianapolis, Indiana, Webb's boyhood friend who died in the service of his country) + Latin "orbis" (disk).
Gender: masculine.
Description

Genitalia: left lateral pilaster obsolete; right lateral pilaster thick, height twice the width; chalice moderately deep and **seated atop a barrel-shaped, solid pedestal;** dorsal, ventral and peripheral structures absent.

Shell: size medium (diameter 15-20 mm); shape globose (height/diameter, 0.7-0.8); umbilicus imperforate; parietal denticle absent; basal denticle absent; palatal denticle absent; periostracal hairs or scales absent; basal lip of aperture straight and pointing downward to make aperture somewhat triangular.

Patera pennsylvanica (Green, 1827)
(Figs. 10b, 45c,d; Table 2; Fig. 52)

(1) Ohio: Pike County (GS-206; FMNH 214703): one live adult, one tissue sampled—dissected (illustrated); electrophoresed. (2) Ohio: Pike County (SC-246; FMNH 214704): one live adult, one tissue sample—illustrated shell.

Subgenus *Vesperpatera*, subgen. nov.
(Figs. 22-25, 48a,b, 49, 50; Table 2; Fig. 52)

Type species: *Polygyra binneyana* Pilsbry, 1899.
Etymology: Latin "vesper" (west) + "patera" (saucer), because all known members occur west of the Mississippi River.
Gender: feminine.
Description

Genitalia: left lateral pilaster variable to inconspicuous or absent; right lateral pilaster long, cord-like; chalice a simple hood or spatula-shaped, right wall high and rounded; dorsal, ventral and peripheral structures absent.

Shell: size medium (diameter 14-26 mm); shape depressed-globose (height/diameter, 0.5-0.6); umbilicus imperforate to narrow and open; parietal denticle small to absent; basal denticle absent; palatal denticle absent; periostracal hairs or scales absent; aperture a smooth oval.

Species Group *Patera binneyana* (Pilsbry, 1899)

Description

Genitalia: left lateral pilaster variable to inconspicuous or absent; right lateral pilaster long, cord-like, usually variable in width; chalice a simple hood; dorsal, ventral and peripheral structures absent.

Shell: size medium (diameter 14-26 mm); shape depressed-globose (height/diameter, 0.5-0.6); umbilicus imperforate to narrow and open; parietal denticle absent to weakly present; basal denticle absent; palatal denticle absent; periostracal hairs or scales absent; aperture a smooth oval, upper margin of apertural lip abruptly reflected so that the **lip is uniform in width.**

Included species

Patera binneyana (Pilsbry, 1899)
(Figs. 22a, 23, 24, 48a,b, 49a,b; Table 2; Fig. 52)

(1) Oklahoma: LeFlore County (GS-89; FMNH 214625): no live adults, 20 tissue samples—electrophoresed #1, 3, 4, 18, 19. (2) Arkansas: Yell County (GS-95; FMNH 214626): one live adult, ?two tissue samples—dissected #2 (illustrated). (3) (Indian Territory: Sugarloaf Mountain) (ANSP-A2278-F): six live adults—dissected one. (4) Arkansas: (Petit Jean) (ANSP A2285): six live adults—dissected one. (5) Arkansas: Yell County (ANSP-A2299-C): four live adults—dissected one. (6) Arkansas: Polk County (FMNH 176008): three live adults—dissected #C (illustrated, both dissected and undissected); examined #A, previously dissected by Solem (1976); removed and examined genitalia of #B; illustrated shell #B. (7) Arkansas: Polk County (FMNH 176018): one live adult—dissected to examine penial length. (8) Arkansas: Polk County (FMNH 176169): two live adults—dissected one to examine penial length. (9) Arkansas: Scott County (FMNH 176195): one live adult—dissected to examine penial length. (10) Arkansas: Polk County (Hubricht 31615): two live adults—dissected both to examine penial length; illustrated shell (Hubricht 31621) #A. (11) Arkansas: Polk County (Hubricht 33898) three live adults—dissected one to examine penial length.

Variation: There are two distinct penial lengths in *P. binneyana*. A relatively short penis (Fig. 22a, length 32.4 mm; Pilsbry 1940: Fig. 445D, length 33 mm) occurs in sampled populations #2, 3, 5, 7, 10 and 11, and a slightly longer penis occurs in populations #4 and 8. In populations #6 and 9, however, the penis is extremely long (Figs. 23, 24, length 91.0 mm; Solem 1976: Fig. 7, length >100 mm). W. L. Pratt reported (*in litt.* to Alan Solem, 8 November 1982) that the short-penis form has radular teeth with "extremely elongate, slender and bladelike [mesocones on the radular teeth], very different from [the mesocones of the long-penis form as illustrated in Solem 1976, Figs. 18-21]." Thus, *P. binneyana* is almost certainly two separate species, which for the time being will be referred to as *binneyana* "short" and *binneyana* "long."

Patera indianorum (Pilsbry, 1899)
(Fig. 25; Table 2; Fig. 52)

(1) Oklahoma: Atoka County (GS-87; FMNH 214665): two live adults, 14 tissue samples—dissected #1, 5 (illustrated #1); electrophoresed #1, 5, 6, 8.

Patera clenchi (Rehder, 1932)
(Figs. 25a, 50a,b; Table 2; Fig. 52)

(1)? Arkansas: Izard County (GS-97; FMNH 214652): no live adults, one tissue sample—electrophoresed. (2) Arkansas: Izard County (Hubricht 25210): one live adult—dissected (illustrated); illustrated shell.

Patera kiowaensis (Simpson, 1888)
(Figs. 25c, 50c,d; Table 2; Fig. 52)

(1) Oklahoma: Atoka County (GS-84; FMNH 214684): ca. nine live adults, 19 tissue samples—dissected #12, 18 (illustrated #12); electrophoresed #1, 6, 9, 16; illustrated shell #7.

Species Group *Patera roemeri*
(Pfeiffer, 1848)

Description

Genitalia: left lateral pilaster inconspicuous or absent; right lateral pilaster long, cord-like, usually uniform in width; chalice spatula-shaped, **right wall high and rounded,** left wall reduced; dorsal, ventral and peripheral structures absent.

Shell: size medium (diameter 15-24 mm); shape depressed-globose (height/diameter, 0.5-0.6); umbilicus imperforate to narrow and creviced; parietal denticle absent to weakly present; basal denticle absent; palatal denticle absent; periostracal hairs or scales absent; aperture a smooth oval, **upper margin of apertural lip straight and unreflected.**

Included species

Patera roemeri (Pfeiffer, 1848)
(Figs. 22c, 49e,f; Table 2; Fig. 52)

(1) Texas: Bastrop County (GS-63; FMNH 214718): ca. ten live adults, 23 tissue samples—dissected #4, 6, 7, 15, 21 (illustrated #21); electrophoresed #2, 3; illustrated shell #4. (2) Texas: Travis County (GS-69; FMNH 214719): ca. ten live adults, 25 tissue samples—electrophoresed #1, 8, 10, 12, 15.

Patera leatherwoodi (Pratt, 1971)
(Figs. 22b, 49c,d; Table 2; Fig. 52)

(1) Texas: Travis County (GS-67; FMNH 214692): one live adult, one tissue sample—dissected (illustrated); electrophoresed; illustrated shell. (2) Texas: Travis County (GS-68; FMNH 214693): one live adult, one tissue sample—dissected; electrophoresed.

Subgenus *Patera s. str.*
(Figs. 19-21, 25, 47, 50c,d;
Table 2; Fig. 52)

Description

Genitalia: left lateral pilaster cord-like, running entire length of penis; right lateral pilaster variable; chalice a simple hood; dorsal structures generally absent, rarely present as thin, parallel, anastomosing dorsal cords; ventral and peripheral structures absent.

Shell: size medium (diameter 13-27 mm); shape generally depressed (height/diameter, 0.4-0.6), rarely globose (height/diameter, 0.7 mm); umbilicus imperforate, broadly covered; parietal denticle pronounced, blade-like; basal denticle present as long, thin lamella, palatally truncated; palatal denticle absent; periostracal hairs or scales absent.

Species Group *Patera perigrapta*
(Pilsbry, 1894)
(Figs. 21, 46; Table 2; Fig. 52)

Description

Genitalia: left lateral pilaster extending full length of penis; right lateral pilaster extending half to full length of penis; chalice a simple hood; dorsal, ventral and peripheral structures absent.

Shell: size medium (16-23 mm); shape **depressed** (height/diameter, 0.4-0.5); umbilicus imperforate; parietal denticle pronounced, blade-like; basal denticle present as long, thin lamella; palatal denticle absent; periostracal hairs or scales absent; inter-strial microsculpture of conspicuous **incised spiral lines.**

Included species

Patera perigrapta (Pilsbry, 1894)
(Figs. 21b, 46c,d; Table 2; Fig. 52)

(1) Tennessee: Blount County (GS-3; FMNH 214705): ca. one live adult, 15 tissue samples—dissected #12; electrophoresed #1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 14. (2) Tennessee: Blount County (GS-9; FMNH 214707): ca. five live adults, 13 tissue samples—electrophoresed #1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 13. (3) Alabama: Perry County (GS-57; FMNH 214708): one live adult, one tissue sample—dissected #A. (4) Arkansas: Crawford County (GS-90; 214709): 13 live adults, 13 tissue samples—dissected #1. (5) Arkan-

sas: Izard County (GS-98; FMNH 214710) 21 live adults, 21 tissue samples—dissected #8, 20, A (illustrated #8); examined partly everted penes of #7, 9, 18; electrophoresed #5, 7, 8, 9, 21; illustrated shell #3. (6) South Carolina: Lee County (GS-170; FMNH 214712): one live adult—examined everted penis. (7) Alabama: Cleburne County (SC-61; FMNH 214713): two live adults—examined everted penis of one specimen. (8) Alabama: Cleburne County (SC-65; FMNH 214714): one live adult—examined everted penis. (9) Alabama: Cleburne County (SC-66; FMNH 214715): one live adult—examined everted penis. (10) Alabama: DeKalb County (SC-67; FMNH 214716): four live adults—examined everted penes of four specimens. (11) Tennessee: Marion County (SC-97; FMNH 214717): two live adults—examined everted penes of two specimens.

Patera panselena Hubricht, 1976
(Figs. 21a, 46a,b; Table 2; Fig. 52)

(1) West Virginia: Boone County (GS-142; FMNH 214700): 11 live adults, 11 tissue samples—dissected #2, 6, 9 (illustrated #9); electrophoresed #1, 4, 5, 10, 11; illustrated shell #A. (2) West Virginia: Kanawha County (GS-204; FMNH uncataloged): one live adult, one tissue sample—electrophoresed.

Species Group *Patera appressa* (Say, 1821)
(Figs. 19a,c, 20, 47a,b,e,f, 49c,d; Table 2; Fig. 52)

Description

Genitalia: left lateral pilaster extending full length of penis; right lateral pilaster variable; chalice a simple hood; dorsal structures absent or present as parallel, sometimes anastomosing cords; ventral and peripheral structures absent.

Shell: size medium (15-27 mm); shape **depressed** (height/diameter, 0.4-0.5); umbilicus imperforate; parietal denticle pronounced, blade-like; basal denticle present as long, thin lamella; palatal denticle absent; periostracal hairs or scales absent; inter-strial microsculpture generally **smooth or pustular.**

Included species

Patera appressa (Say, 1821)
(Figs. 19c, 47e,f; Table 2; Fig. 52)

(1) Kentucky: McCreary County (GS-12; FMNH 214619): 12 live adults, 12 tissue samples—electrophoresed #1, 2, 3, 4, 5, 6, 7, 8, 9, 10. (2) Kentucky: Pulaski County (GS-13; FMNH uncat.): unknown number of live adults, 30 tissue samples—electrophoresed #11, 12, 13, 14, 15, 16, 17, 18, 19, 20, 22, 23, 25. (3) Tennessee: Franklin County (GS-104; FMNH 214620): six live adults, eight tissue samples—dissected #1, 5, 7 (illustrated #1); illustrated shell #2. (4) Tennessee: Overton County (GS-111; FMNH 214621); ca. three live adults, nine tissue samples—electrophoresed #2, 3, 4, 6, 7. (5) West Virginia: Summers County (GS-141; FMNH 214622): ten live adults, ten tissue samples—dissected #2, 4, 6, 8.

Patera laevior (Pilsbry, 1940)
(Figs. 20, 48c,d; Table 2; Fig. 52)

(1) Kentucky: Hancock County (H-22; FMNH 214685): three live adults—dissected #1, 3, A (illustrated #1, 3); illustrated shell #3. (2) Indiana: Jefferson County (GS-14; FMNH 214687): no live adults, 16 tissue samples—electrophoresed #1, 2, 3, 4, 5, 6, 7, 8, 9, 10. (3) Kentucky: Fayette County (GS-112; FMNH 214689): no live adults, 11 tissue samples—electrophoresed #1, 4, 6. (4) Kentucky: Edmonson County (GS-125; FMNH 214690): five live adults, five tissue samples—dissected #1, 4, 5; electrophoresed #1, 2, 3, 4. (5) Illinois: Hardin County (SC-217; FMNH 214691): two live adults—examined everted penes of three specimens.

Patera sargentiana (Johnson & Pilsbry, 1892)
(Figs. 19a, 47a,b; Table 2; Fig. 52)

(1) Alabama: Madison County (GS-20; FMNH 214728): no live adults, 20 tissue samples—electrophoresed #1, 2, 3, 4, 5, 6, 7, 8, 9, 10. (2) Alabama: Madison County [GS-101 (= GS-20); FMNH 214729]: 12 live adults, 12 tissue samples—dissected #1, 9, 12 (illustrated #1); electrophoresed #2, 5, 8, 9; illustrated shell #2.

Species Group *Patera clarki* (Lea, 1858)
(Figs. 19b, 47c,d; Table 2; Fig. 52)

Description

Genitalia: left lateral pilaster extending full length of penis; right lateral pilaster extending entire length of penis; chalice a simple hood; dorsal, ventral and peripheral structures absent.

Shell: size medium (13-18 mm); shape **globose** (height/diameter, 0.7); umbilicus imperforate; parietal denticle pronounced, bladelike; basal denticle present as long, thin, truncate lamella; palatal denticle absent; periostracal hairs or scales absent; inter-strial microsculpture generally smooth, base **sometimes malleate.**

Included species

Patera clarki (Lea, 1858)
(Figs. 19b, 47c,d; Table 2; Fig. 52)

(1) Tennessee: Sevier County (GS-6; FMNH 214633): no live adults, three tissue samples—electrophoresed #1, 2, 3. (2) North Carolina: Haywood County (GS-10; FMNH 214634): five live adults, 14 tissue samples—dissected #1, 2, 3, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14. (3) North Carolina: Swain County (GS-1; FMNH 214632): ca. seven live adults, 11 tissue samples—dissected #5, 6, 7; electrophoresed #1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11.

Genus *Inflectarius* Pilsbry, 1940
(Figs. 9a,c, 10a, 11a, 12-14, 35a,b, 40a,b,e,f, 43,44c,d, 45a,b; Table 2; Fig. 52)

Type species: *Helix inflecta* Say, 1821, by original designation.

Etymology: Latin "inflecta" (name of type species) + "-arius" (Latinizing suffix).

Gender: masculine.

Definition

Genitalia: left lateral pilaster variable; right lateral pilaster variable; third pilaster present or absent; chalice generally a simple hood, rarely (only in *I. ferrissi*) shaped like a thick spoon; dorsal structures absent (except for third pilaster, when present); ventral and peripheral structures absent.

Shell: size **generally small,** rarely medium (diameter 8-25 mm); shape subglobose to globose (height/diameter, 0.5-0.7); umbilicus narrow, broadly or narrowly covered, rarely creviced; parietal denticle generally pronounced, small or absent; basal denticle present or absent, rarely as a trace lamella; palatal denticle pronounced, reduced or absent, flush with the aperture or, rarely, recessed; **periostracal scales** present (three types) or absent; body whorl with or without crest before preapertural deflection.

Comparisons

Shell. *Inflectarius* is the only genus in the Mesodontini with a palatal apertural tooth and the only member of the Mesodontini with scale-like periostracal hairs (the hirsute members of *Fumonelix* have thin, rounded hairs that are not scale-like, except for *F. wetherbyi*, which species can be confusing). Only three species of *Inflectarius* lack hairs: *I. ferrissi*, *I. downieanus* and *I. kalmianus*. Of these, the shell of *I. ferrissi* is distinctively unlike that of any of the other Mesodontini. On the other hand, the shells of *I. downieanus* and *I. kalmianus* are very much convergent on those of *Mesodon* (*Akromesodon*) and on those of *Fumonelix wheatleyi;* they can be distinguished by their smaller size and by the unique structure of the umbilicus, which is either barely creviced (*I. kalmianus*) or deeply imperforate with the apertural lip plunging deeply into the umbilical pit (*I. downieanus*). The shells of many species of the genus *Triodopsis* Rafinesque, 1819 (Emberton, 1988) resemble those of the tridentate *Inflectarius*, but shells of *Triodopsis* are always umbilicate and never hirsute, whereas shells of the tridentate species of *Inflectarius* are always imperforate and always hairy. The shell of *I. ferrissi* is very similar to that of the triodopsine *Neohelix dentifera* (Binney, 1837) (Emberton, in press).

Subgenus *Hubrichtius*, subgen. nov.
(Figs. 10a, 11a, 35a,b, 45a,b; Table 2; Fig. 52)

Type species: *Mesodon kalmianus* Hubricht, 1965.

Etymology: Hubricht (Mr. Leslie Hubricht of Meridian, Mississippi, an expert on the land snails of eastern North America) + Latin "-ius" (Latinizing suffix).

Gender: masculine.

Description

Genitalia: left lateral pilaster variable; right lateral pilaster variable; chalice a simple hood; dorsal, ventral and peripheral structures absent.

Shell: size small (diameter 9-15 mm); shape globose (height/diameter, 0.7); umbilicus narrow, narrowly covered, sometimes creviced; parietal denticle absent; basal denticle absent; palatal denticle absent; periostracal hairs or scales absent; body whorl lacking crest before preapertural deflection.

Included species

Inflectarius downieanus (Bland, 1861)
(Figs. 10a, 45a,b; Fig. 52)

(1) Alabama: DeKalb County (Hubricht 30825): unknown number of live adults—dis-

sected #A, B (illustrated #B); illustrated shell #A.

Inflectarius kalmianus Hubricht, 1965
(Figs. 11a, 35a,b; Table 2; Fig. 52)

(1) Kentucky: Knox County [GS-116; FMNH 214683 (the specimens in this lot are unusually numbered from having been confused in the field with microsympatric *Mesodon clausus*)]: three live adults, 3 tissue samples—dissected #13, A (illustrated #13); electrophoresed #18; illustrated shell #18. (2) Kentucky: Knox County [GS-188 (= GS-116); FMNH 214682]: five live adults, five tissue samples—dissected #2, A; electrophoresed #1, 2, 3, 4.

Subgenus *Inflectarius s. str.*
(Figs. 9a,c, 12, 13b, 14, 40a,b,e,f, 43, 44c,d; Table 2; Fig. 52)

Description

Genitalia: left lateral pilaster variable; right lateral pilaster variable; third pilaster present or absent; chalice generally a simple hood, rarely (only in *I. ferrissi*) shaped like a thick spoon; dorsal structures absent (except for third pilaster, when present); ventral and peripheral structures absent.

Shell: size generally small, rarely medium (diameter 8-25 mm); shape subglobose (height/diameter, 0.5-0.6); umbilicus narrow, **broadly covered;** parietal denticle generally long and pronounced, rarely (only in *I. ferrissi*) short and small; basal denticle generally a tooth, rarely absent or as a trace lamella; palatal denticle pronounced, reduced or absent, flush with the aperture or, rarely, recessed; periostracal hairs or scales present (three types) or, rarely (only in *I. ferrissi*) absent; body whorl with or without crest before preapertural deflection.

Remarks. The highly derived shell of *I. ferrissi* is correlated with its extremely specialized ecology (Emberton, in press).

Species Group *Inflectarius edentatus* (Sampson, 1889)
(Figs. 12b,c, 43c,f; Table 2; Fig. 52)

Description

Genitalia: left lateral pilaster variable; right lateral pilaster variable; chalice a simple hood; dorsal, ventral and peripheral structures absent.

Shell: size small (diameter 13-14 mm); shape subglobose (height/diameter, 0.5-0.6); umbilicus narrow, broadly covered; parietal denticle long and pronounced; basal denticle a slight bump; palatal denticle a slight bump, flush with aperture; periostracal hairs or scales present, low, rounded, and blunt; body whorl with pronounced crest before preapertural deflection.

Included species

Inflectarius edentatus (Sampson, 1889)
(Figs. 12c, 43e,f; Table 2; Fig. 52)

(1) Arkansas: Crawford County (GS-90; FMNH 214653): 12 live adults, 12 tissue samples—dissected #2, 7, 9 (illustrated #2); electrophoresed #1, 6, 10; illustrated shell #A. (2) Arkansas: Crawford County (GS-91; FMNH 214654): ca. three live adults, eight tissue samples—electrophoresed #2, 7, 9(?)

Inflectarius magazinensis (Pilsbry & Ferriss, 1907)
(Figs. 12b, 43c,d; Table 2; Fig. 52)

(1) Arkansas: Yell County (GS-95; FMNH 214695): ca. 20 live adults, 26 tissue samples—dissected #5, 6, 14 (illustrated #5); electrophoresed #2, 4, 12, 18; illustrated shell #17.

Remarks. Clench & Turner (1962) gave the date of publication for this species as 1907. Their judgement has been followed here.

Species Group *Inflectarius smithi* (Clapp, 1905)
(Figs. 9c, 40e,f; Table 2; Fig. 52)

Description

Genitalia: left lateral pilaster extending less than half length of penis; right lateral pilaster extending full length of penis, expanding basally as massive bulge; chalice a simple hood; dorsal, ventral and peripheral structures absent.

Shell: size medium (diameter 14-17 mm); shape subglobose (height/diameter, 0.6); umbilicus narrow, broadly covered; parietal denticle long and pronounced; basal denticle present as long, thin lamella truncated at palatal end; palatal denticle pronounced, broad, flush with apertural lip; periostracal hairs or scales present, very dense, long and sharply pointed; body whorl lacking crest before preapertural deflection.

Included species

Inflectarius smithi (Clapp, 1905)
(Figs. 9c, 40e,f; Table 2; Fig. 52)

(1) Alabama: Madison County (GS-20; FMNH 214736): two live adults, 11 tissue samples—electrophoresed #1, 2, 3, 4, 5, 6, 7, 8, 9, 10; illustrated shell #1. (2) Alabama: Madison County [GS-101 (=GS- 20); FMNH 214737]: five live adults, five tissue samples—dissected #1, 2, 4 (illustrated #4); electrophoresed #2, 3, 4. (3) Tennessee: Franklin County (GS-104; FMNH 214738): seven live adults, seven tissue samples—electrophoresed #1, 2, 7.

Species Group *Inflectarius inflectus* (Say, 1821)
(Figs. 9a, 12a, 13b, 14, 40a,b, 43a,b, 44c,d; Table 2; Fig. 52)

Description

Genitalia: left lateral pilaster variable; right lateral pilaster variable; third pilaster sometimes present; chalice a simple hood; dorsal, ventral and peripheral structures absent.

Shell: size small (diameter 8-16 mm); shape subglobose (height/diameter, 0.5-0.6); umbilicus narrow, broadly covered; parietal denticle long and pronounced; basal denticle a pronounced tooth or rarely absent; palatal denticle a pronounced tooth, either flush with aperture or moderately recessed, or rarely absent; periostracal hairs or scales present, low, bearing central points; body whorl bearing slight crest before preapertural deflection.

Included species

Inflectarius verus Hubricht, 1954
(Fig. 14; Table 2; Fig. 52)

(1) North Carolina: Haywood County (GS-10; FMNH 214756): 14 live adults, 14 tissue samples—dissected #3, 4, 8; electrophoresed #1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13.

Discussion. The status and name of this species are puzzling. Hubricht (1954b) did not illustrate the holotype. The holotype (USNM 607137) has not been examined, but three of the paratypes (ANSP 191211) are definitely *Inflectarius subpalliatus*, under which Hubricht (1985) eventually synonomized *I. verus*. Recently-collected specimens from the type locality of *I. verus* (FMNH 214756), the shells of which have not been illustrated, differ substantially in penial morphology (Fig. 14) from *I. subpalliatus* (Fig. 13a). These provisionally have been called *I. verus*.

Inflectarius inflectus (Say, 1821)
(Figs. 9a, 40a,b; Table 2; Fig. 52)

(1) Kentucky: Henderson County (GS-16; FMNH 214666): ca. 20 live adults, 30 tissue samples—dissected #21, 27, 29; electrophoresed #1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 15, 16, 17, 18, 19, 20, 25, 30. (2) Alabama: Clarke County (GS-53; FMNH 214667): 16 live adults, 16 tissue samples—electrophoresed #1, 2, 3, 4, 11, 16. (3) Oklahoma: LeFlore County (GS-89; FMNH 214668): 30 live adults, 30 tissue samples—electrophoresed #9, 11. (4) Arkansas: Yell County (GS-95; FMNH 214670): one live adult, one tissue sample—dissected. (5) Alabama: Madison County (SC-26; FMNH 214674): one live adult—dissected. (6) Tennessee: Blount County (SC-130; FMNH 214672): 12 live adults, 12 tissue samples—dissected #2, 3, 8 (illustrated #2); illustrated shell #1.

Inflectarius rugeli (Shuttleworth, 1852)
(Figs. 13b, 44c,d; Table 2; Fig. 52)

(1) Tennessee: Swain County (GS-3; FMNH 214720): 11 live adults, 11 tissue samples—dissected #5, 10, A; electrophoresed #1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11. (2) Tennessee: Polk County (GS-106; FMNH uncat.): unknown number of live adults, nine tissue samples—electrophoresed #1, 3, 4, 5, 6. (3) Alabama: Cleburne County (GS-180; FMNH 214725): ten live adults, ten tissue samples—electrophoresed #1, 2, 3, 6, 8. (4) Tennessee: Blount County (SC-130; FMNH 214726): eight live adults, eight tissue samples—dissected #2, 3, 4 (illustrated #2); illustrated shell #8.

Inflectarius approximans (Clapp, 1905)
(Figs. 12a, 43a,b; Table 2; Fig. 52)

(1) Alabama: Perry County (GS-57; FMNH 214623): one live adult, one tissue sample—dissected (illustrated); electrophoresed. (2) Alabama: Perry County (Hubricht 23497): unknown number of live adults—dissected #A; illustrated shell #A.

Species Group *Inflectarius ferrissi* (Pilsbry, 1897)
(Figs. 13a,c, 44a,b,e,f; Table 2; Fig. 52)

Description

Genitalia: left lateral pilaster variable; right lateral pilaster variable; third pilaster present; chalice variable; dorsal ventral and peripheral structures absent.

Shell: size medium (diameter 13-25 mm); shape subglobose (height/diameter, 0.5-0.6); umbilicus narrow, broadly covered; parietal denticle small and short to pronounced and long; basal denticle absent or present as an inconspicuous long, thin lamella, truncated palatally; palatal denticle absent; periostracal hairs or scales present, low and bearing central points, to entirely absent; body whorl lacking crest before preapertural deflection.

Included species

Inflectarius subpalliatus (Pilsbry, 1893)
(Figs. 13a, 44a,b; Table 2; Fig. 52)

(1) Tennessee: Carter County (GS-11; FMNH 214739): one live adult, one tissue sample—electrophoresed. (2) North Carolina: Avery County (GS-153; FMNH 214740): six live adults, 11 tissue samples—dissected #1, 2, 3 (illustrated #2); electrophoresed #2, 3, 4, 5, 8; illustrated shell #8.

Inflectarius ferrissi (Pilsbry, 1897)
(Figs. 13c, 44e,f; Table 2; Fig. 52)

(1) North Carolina: Swain County (GS-1; FMNH 214657): ca. seven live adults, ten tissue samples—electrophoresed #1, 2, 3, 4, 5, 6, 7, 8, 9, 10. (2) Tennessee-North Carolina: Blount-Swain Counties (GS-2; FMNH 214658): ca. two live adults, 11 tissue samples—electrophoresed #1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11. (3) Tennessee-North Carolina: Blount-Swain Counties (GS-5; FMNH 214659): three live adults, four tissue samples—dissected #1, 3, 4 (illustrated #3); electrophoresed #1, 2, 3, 4. (4) Tennessee-North Carolina: Blount-Swain Counties [SC-144 (= GS-5); FMNH 214661]: ca. six live adults—illustrated shell #A. (5) Tennessee: Sevier County (SC-216; FMNH 214664): 13 live adults, 13 tissue samples—dissected #2, 3, 6.

Genus *Fumonelix* gen. nov.
(Figs. 7, 8, 9b, 40c,d, 41, 42; Table 2; Fig. 52)

Type species: *Helix wheatleyi* Bland, 1860.
Etymology: Latin "fumosa" (smoky) + "montana" (of mountains) + "helix" (snail), hence "snail of the Smoky Mountains."
Gender: feminine.
Description

Genitalia: left lateral pilaster variable; right lateral pilaster variable; **chalice a thick-walled, hooded cup;** dorsal surface with or without a single or at most a pair of bulges; ventral surface with or without a bulge in midline; peripheral structures absent.

Shell: size very small to medium (diameter 8-23 mm); shape subglobose to globose (height/diameter, 0.6-0.7); umbilicus narrow, broadly to narrowly covered; parietal denticle pronounced to absent; basal denticle a faint trace of long, thin lamella, or entirely absent; palatal denticle absent; periostracum with or without thin, rounded hairs or broad, obtusely pointed scales.

Comparisons.

See the Comparisons under *Patera* and *Inflectarius*.

Species Group *Fumonelix wetherbyi* (Bland, 1874)
(Figs. 9b, 40c,d; Table 2; Fig. 52)

Description

Genitalia: left lateral pilaster a humped ridge about half length of penis; right lateral pilaster full-length, **extremely high-standing, and rolled over in inverted penis;** chalice a deep, thin-walled, cylindrical cup; dorsal, ventral and peripheral structures absent.

Shell: size medium (diameter 17-18 mm); shape subglobose (height/diameter, 0.6); umbilicus narrow, broadly covered; parietal denticle pronounced; basal denticle a faint trace of long, thin lamella; palatal denticle absent; **periostracal scales present, small, low, broad and obtusely pointed.**

Included species

Fumonelix wetherbyi (Bland, 1874)
(Figs. 9b, 40c,d; Table 2; Fig. 52)

(1) Kentucky: McCreary County (GS-115; FMNH 214757): eight live adults, 20 tissue samples— dissected #1, 2, 7, 20 (illustrated #20); electrophoresed #2, 3, 4, 5, 8, 11; illustrated shell #4.

Species Group *Fumonelix christyi* (Bland, 1860)
(Figs. 8a, 41; Table 2; Fig. 52)

Description

Genitalia: left lateral pilaster short and thin;

right lateral pilaster long and thin; chalice a thick-walled, hooded cup; dorsal surface with thick, long bulge on right side; ventral and peripheral structures absent.

Shell: size **very small** (diameter 8-9 mm); shape subglobose to globose (height/diameter, 0.6-0.7); umbilicus narrow, broadly covered; parietal denticle pronounced; basal denticle a faint trace of long, thin lamella; palatal denticle absent; **periostracal hairs or scales absent.**

Included species

Fumonelix christyi (Bland, 1860)

(Figs. 8a, 41; Table 2; Fig. 52)

(1) North Carolina: Burke County (GS-161; FMNH 214631): ten live adults, 11 tissue samples—dissected #2, 5, 6 (illustrated #6); electrophoresed #1, 2, 3, 4, 6, 8, 9, 10, 11; illustrated shell #10.

Species Group *Fumonelix wheatleyi* (Bland, 1860)

(Figs. 8b-d, 42; Table 2; Fig. 52)

Description

Genitalia: left lateral pilaster variable; right lateral pilaster variable; chalice a thick-walled, hooded cup; dorsal surface plain, with peripheral-apical bulges, or with basal bulge formed by fusion of left and right lateral pilasters; **mid-ventral surface with conspicuous bulge;** peripheral structures absent.

Shell: size small to medium (diameter 13-23 mm); shape subglobose to globose (height/diameter, 0.6-0.7); umbilicus narrow, broadly to narrowly covered; parietal denticle pronounced to absent; basal denticle a faint trace of long, thin lamella, or entirely absent; palatal denticle absent; **periostracal hairs sometimes present, thin, and rounded,** or absent.

Discussion.

This group requires revision as soon as possible, because it includes three described species of potentially endangered status—*F. jonesiana, F. archeri* and *F. orestes*—and because *F. wheatleyi* (q.v.) seemingly includes at least one other cryptic species, which also might be rare. F. G. Thompson's unpublished study assembled much alcohol-preserved material now housed in the Florida State Museum.

Included species

Fumonelix wheatleyi (Bland, 1860)

(Figs. 8c, 42a,b, 51; Table 2; Fig. 52)

(1) Tennessee: Sevier County (GS-6; FMNH uncat.): unknown number of live adults, unknown number of tissue samples—dissected #1, 3, 5 (illustrated #5); electrophoresed #1, 2, 3, 4, 5, 6, 7, 8, 9, 10; illustrated shell #3. (2) North Carolina: Haywood County (GS-10; FMNH uncat.): unknown number of live adults, 21 tissue samples—dissected #2, 9, 12; electrophoresed #1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 18, 21. (3) North Carolina: Avery County (GS-153; FMNH 214767): ten live adults, ten tissue samples—dissected #4, 7, 10; electrophoresed #1, 3, 4, 5, 6, 8. (4) Tennessee-North Carolina: Sevier-Swain Counties (SC-144; FMNH 214762): two live adults, two tissue samples—dissected #1, 2. (5) North Carolina: Swain County (SC-192; FMNH 214763): one live adult, three tissue samples—dissected #3. (6) North Carolina: Macon County (SC-202; FMNH 214766): two live adults, two tissue samples—dissected #1, 2. (7) North Carolina: Macon County (SC-212; FMNH 214768): two live adults, two tissue samples—dissected #2.

Fumonelix jonesiana (Archer, 1938)

(Figs. 8b, 42c,d; Table 2; Fig. 52)

(1) North Carolina: Swain County (GS-1; FMNH 214678): two live adults, ten tissue samples—dissected #2, 10. (2) Tennessee: Sevier County (SC-155; FMNH 214679): ten live adults, ten tissue samples—dissected #4, 5, 9 (illustrated #5); illustrated shell #3.

Fumonelix orestes (Hubricht, 1975)

(Figs. 8d, 42e,f; Table 2; Fig. 52)

(1) North Carolina: Haywood County (GS-86; FMNH 214698): two live adults, nine tissue samples—dissected #2, 4 (illustrated #4); electrophoresed #1, 3, 4, 5. (2) North Carolina: Haywood County (Hubricht 40465): unknown number of live adults—illustrated shell #A.

Fumonelix archeri (Pilsbry, 1940)

(Fig. 7; Fig. 52)

(1) Tennessee: Polk County (SC-279; FMNH uncat.): three live adults, two tissue samples—dissected #A, B.

Genus *Mesodon* Férussac, 1821
(Figs. 1-6, 11b,c, 15-18, 35c-f, 36-39; Table 2; Fig. 52)

Type species: *Helix thyroidus* [*sic*] Say, 1817, by monotypy (see Taxonomic History).
Etymology: Greek "mesos" (middle) + "odon" (tooth).
Gender: masculine.
Description

Genitalia: left lateral pilaster rounded or cord-like, variable in length; right lateral pilaster rounded or cord-like, variable in length or absent; chalice variable, **left wall higher than right;** dorsal cords or ridges present, with or without enlarging into basal bulges, or absent; ventral structures generally absent, rarely present as a mid-ventral pouch; peripheral structures generally absent, rarely present as a shoulder.

Comparisons.

East of the Mississippi River, *Mesodon* contains all of the globose Mesodontini except for *Patera pennsylvanica, P. clarki, Inflectarius downieanus, I. kalmianus, Fumonelix wheatleyi* and *F. orestes,* and it contains all of the broadly umbilicate Mesodontini. Only four species of *Mesodon* occur west of the Mississippi (*M. zaletus, M. elevatus, M. clausus* and *M. thyroidus;* (Fig. 51). Of these, only *M. thyroidus* might be confused with any other western member of the Mesodontini, primarily *Patera roemeri,* with which it is sometimes sympatric; but *Mesodon thyroidus* is usually easily distinguished by its higher spire and duller surface. Several of the large, globose, toothless species of *Mesodon*—especially *M. normalis,* the toothless morph of *M. zaletus* and the imperforate and toothless morph of *M. thyroidus* (subspecies *bucculentus*)—are very readily confused with species of the triodopsine genus *Neohelix* (Pilsbry, 1940; Solem, 1976; Emberton, 1988).

Subgenus *Appalachina* Pilsbry, 1940
(Figs. 18a,b, 39; Table 2; Fig. 52)

Type species: *Polygyra sayana* Pilsbry, in Pilsbry & Ferriss, 1906, by original designation.
Etymology: Appalachia (the major mountainous region of eastern North America) + Latin "-ina" (Latinizing suffix).
Gender: feminine.
Description

Genitalia: left lateral pilaster rounded, variable in length; right lateral pilaster present or absent; chalice somewhat spatulate, the left wall high and even; dorsal, ventral and peripheral structures absent.

Shell: size large (diameter 19-40 mm); shape subglobose (height/diameter, 0.6); **umbilicus wide, open;** parietal denticle small or absent; basal denticle a basocolumellar peg, or absent; palatal denticle absent; periostracal hairs or scales absent.

Included species

Mesodon sayanus
(Pilsbry, in Pilsbry & Ferriss, 1906)
(Figs. 18a, 39c,d; Table 2; Fig. 52)

(1) Kentucky: Harlan County (GS-122; FMNH 214732): no live adults, ten tissue samples—electrophoresed #2, 3, 4, 5, 7, 8, 9, 10. (2) West Virginia: Preston County (GS-130; FMNH 214734): three live adults, seven tissue samples—dissected #1, 4, 6 (illustrated #6); electrophoresed #3, 5; illustrated shell #7.

Mesodon chilhoweensis (Lewis, 1870)
(Figs. 18b, 39a,b; Table 2; Fig. 52)

(1) Tennessee: Blount County (GS-3; FMNH 214627): ca. two live adults, 20 tissue samples—electrophoresed #1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 12, 13, 14, 15, 20. (2) Tennessee: Blount County (GS-9; FMNH 214628): ca. one live adult, ten tissue samples—electrophoresed #1, 2, 3, 4, 5, 6, 7, 8, 9, 10. (3) North Carolina: Graham County (SC-263; FMNH 214630): two live adults—dissected #A. (4) Tennessee: Sevier County (Hubricht 30943): unknown number of live adults—dissected #A (illustrated); illustrated shell #A.

Subgenus *Aphalogona* Webb, 1954b
(Figs. 1-6, 16a, 17, 37a,b, 38; Table 2; Fig. 52)

Type species: *Helix elevata* Say, 1821, by original designation.
Etymology: Greek "a-" (without) + "phalos" (shining) [error for "lophos" (crest)] + "gona" [error for "gone" (that which produces seed), incorrectly translated as "sex organ"], thus, by original intent, "penis without a chalice" (Webb, 1954b: 19).
Gender: feminine.
Description

Genitalia: left lateral pilaster cord-like, extending one-third to full length of penis; right lateral pilaster cord-like, extending two-thirds to full length of penis; chalice either a V-shaped notch defined by massive walls, and which everts whenever penis everts (Webb, 1954b: plate 12, figs. 8, 14-16), or a thin-walled deep, scalloped-edged cylinder atop a solid, cylindrical pedestral; dorsal wall bearing four to ten cord-like, subparallel, anastomosing ridges, running longitudinally to 30 degrees obliquely; mid-ventral pouch present or absent; peripheral structures absent.

Shell: size medium to large (diameter 15-31 mm); shape globose (height/diameter, 0.7-0.8); umbilicus narrow, broadly covered; parietal denticle pronounced to absent; basal denticle a long, thin lamella truncated palatally; palatal denticle absent; periostracal hairs or scales absent.

Remarks.

Webb originally described *Aphalogona* as a section, which, according to the ICZN (1985: article 10e), is nomenclaturally equivalent to a subgenus.

Included species

Mesodon elevatus (Say, 1821)
(Figs. 3f-j, 4f-j, 5d-f, 6d-f, 38c,d;
Table 2; Fig. 52)

(1) Tennessee: Franklin County (GS-104; FMNH 214655): 35 live adults, 35 tissue samples—dissected and illustrated #11, 14, 16, 29, 39; electrophoresed #1, 3, 4, 5, 7, 8, 10, 13, 16, 17, 18, 19, 23, 26, 29, 33, 35, 38; illustrated shell #33. (2) Indiana: Owen County (FMNH 214656): ca. ten live adults—dissected and illustrated #A, B, C.

Variation. Variation in penial morphology (Figs. 3f-j, 4f-j, 5d-f, 6d-f) was discussed above.

Mesodon zaletus (Binney, 1837)
(Figs. 3a-e, 4a-e, 5a-c, 6a-c, 17, 38a,b;
Table 2; Fig. 52)

(1) Tennessee: Blount County (GS-9; FMNH 214771): 17 live adults, 17 tissue samples—dissected #2; Electrophoresed #1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 15, 16, 17. (2) Arkansas: Crawford County (GS-90; FMNH 214787): eight live adults, nine tissue samples (#1, 2, 5-11)—dissected #8; electrophoresed #1, 2, 5, 6, 7, 8, 9, 10, 11. (3) Tennessee: Franklin County (GS-104; FMNH 214774): six live adults, six tissue samples (#2, 6, 11, 12, 22, 27)—dissected and illustrated #2, 6, 12, 22, 27; illustrated undissected penial tubes of #2, 6, 12, 22, 27; illustrated shell #27. (4) Indiana: Owen County (FMNH 214785): ca. ten live adults—dissected and illustrated #A, B, D; illustrated undissected penes of #A, B, D.

Variation. Variation in penial morphology was illustrated (Figs. 3a-e, 4a-e, 5a-c, 6a-c) and discussed previously. Because *M. zaletus* was used as the control for all electrophoresis, it has been tested for the ontogenetic, temporal and geographic stability of alleles (Emberton, 1986; in preparation).

Mesodon mitchellianus (Lea, 1838)
(Figs. 16a, 37a,b; Table 2; Fig. 52)

(1) North Carolina: Henderson County (GS-154; FMNH 214696): eight live adults, eight tissue samples—dissected #1, 5, 6; electrophoresed #1, 2, 4, 5, 6. (2) Ohio: Brown County (Hubricht 19406): unknown number of live adults—dissected #A, B, C (illustrated #B); illustrated shell #A.

Remarks. The North Carolina population represents a significant southward extension of the range of this species presented in Hubricht (1985). This change is incorporated into the range map (Fig. 51).

Subgenus *Akromesodon,* subgen. nov.
(Figs. 1, 2, 11b,c, 15c, 35c-f, 36e,f;
Table 2; Fig. 52)

Type species: *Polygyra andrewsae normalis* Pilsbry, 1900.

Etymology: Greek "akron" (summit, peak) + *Mesodon* (the generic name), because this group not only occupies some of the highest mountain peaks (e.g., Roan Mountain, Virginia, and Clingman's Dome, North Carolina-Tennessee) but also attains the greatest shell size of the entire tribe.

Gender: masculine.

Description

Genitalia: left lateral pilaster cord-like, extending full length of penis; right lateral pilaster present or absent; **chalice a deep, thin-walled scoop, with left wall much higher than right;** dorsal wall bearing eight to 12 cord-like, subparallel, anastomosing ridges, running longitudinally to 30 degrees obliquely, many of which are contiguous with one or both lateral pilasters, and many of which enlarge basally to form a **network of large basal bulges;** ventral and peripheral structures absent.

Shell: size large (diameter 21-40 mm);

shape globose (height/diameter, 0.7-0.8); umbilicus very narrow, broadly covered; parietal denticle generally absent, rarely present as a trace; basal denticle absent; palatal denticle absent; periostracal hairs or scales absent.
Included species

Mesodon andrewsae W. G. Binney, 1879
(Figs. 2, 11b, 35c,d; Table 2; Fig. 52)

(1) Tennessee: Carter County (GS-11; FMNH 214618): 12 live adults, 22 tissue samples—dissected #4, 8 (illustrated #8); examined everted penes of #2, 3 (illustrated #2); illustrated shell #1.

Mesodon normalis (Pilsbry, 1900)
(Figs. 1, 11c, 35e,f; Table 2; Fig. 52)

(1) Tennessee: Blount County (GS-3; FMNH 214979): ca. 25 live adults, 22 tissue samples—electrophoresed #2, 3, 4, 5, 8, 9, 11, 12, 13, 14, 15, 16, 17, 18, 19, 20, 21, 23, 26, 30, 32, 34. (2) North Carolina: Watauga County (GS-200; FMNH 214966): two live adults, four tissue samples—electrophoresed #1, 2, 3, 4. (3) Tennessee: Cocke County (SC-149; FMNH 214970) 12 live adults, 12 tissue samples—dissected #3, 7, 11. (4) Tennessee: Blount County (SC-154; FMNH 214980): 14 live adults, 14 tissue samples—dissected #8, 10, 13. (5) North Carolina: Swain County (SC-158; FMNH 214977): four live adults, four tissue samples—dissected #4 (illustrated); illustrated shell #2. (6) North Carolina: Macon County (SC-184; FMNH 214987): ten live adults, ten tissue samples—dissected #5, 6, 10. (7) North Carolina: Macon County (SC-204; FMNH 214984): nine live adults, nine tissue samples—dissected #2, 3.

Variation. The dissected populations differ considerably in the degree to which the chalice walls are flared.

Mesodon altivagus (Pilsbry, 1900)
(Figs. 15c, 36e,f; Table 2; Fig. 52)

(1) Tennessee: Blount County (GS-2; FMNH 214613): ten live adults, ten tissue samples—electrophoresed #1, 2, 3, 4, 5, 6, 7, 8, 9, 10. (2) Tennessee: Blount County (GS-5; FMNH 214614): 20 live adults, 20 tissue samples—electrophoresed #1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 15, 16, 17, 19, 20. (3) North Carolina: Avery County (GS-205; FMNH 214615): one live adult; one tissue sample—electrophoresed. (4) North Carolina: Swain County (SC-144; FMNH 214616): 12 live adults, 12 tissue samples—dissected #7, 9 (illustrated #7); illustrated shell #7. (5) North Carolina: Swain County (SC-145; FMNH 214617): one live adult, four tissue samples—dissected #4.

Remarks. The penial morphology of *M. altivagus* seems quite different from that of typical *M. andrewsae,* indicating that these are separate species.

Subgenus *Mesodon s. str.*
(Figs. 15a,b, 16b,c, 36a-d, 37c-f;
Table 2; Fig. 52)

Description

Genitalia: left lateral pilaster extending full length of penis, cord-like; right lateral pilaster extending full length of penis, cord-like; **chalice a thick-walled, rounded or pointed ear-like flap, flared to the left, rolled over to right in uneverted penis;** dorsal wall bearing about **eight to 12 thin parallel ridges, equal in diameter, which is constant or gradually increases basally;** ventral structures absent; peripheral step-like shoulder present or absent.

Shell: size medium to large (14-31 mm); shape subglobose to globose (height/diameter, 0.6-0.7); umbilicus narrow, partly to fully and broadly covered; parietal denticle present and small, or absent; basal denticle absent; palatal denticle absent; periostracal hairs or scales absent.

Species Group *Mesodon sanus*
(Clench & Archer, 1933)
(Figs. 15a, 36a,b; Table 2; Fig. 52)

Description

Genitalia: left lateral pilaster extending full length of penis, cord-like; right lateral pilaster extending full length of penis, cord-like; chalice a thick-walled, rounded ear-like flap, flared to left, rolled over to right in uneverted penis; dorsal wall bearing about 12 thin parallel ridges, alike in diameter, which gradually increases basally; ventral and peripheral structures absent.

Shell: size medium (19-20 mm); shape **subglobose** (height/diameter, 0.6); umbilicus narrow, partly covered; parietal denticle absent; basal denticle absent; palatal denticle absent; periostracal hairs or scales absent.
Included species

Mesodon sanus (Clench & Archer, 1933)
(Figs. 15a, 36a,b; Table 2; Fig. 52)

(1) Tennessee: Franklin County (GS-103; FMNH 214727): two live adults, three tissue samples—dissected #1, 2 (illustrated #2); electrophoresed #1, 2, 3; illustrated shell #8.

Species Group *Mesodon thyroidus* (Say, 1817)
(Figs. 15a,b, 16b,c, 36a-d, 37c-f; Table 2; Fig. 52)

Description

Genitalia: left lateral pilaster extending full length of penis, cord-like; right lateral pilaster extending full length of penis, cord-like; chalice a thick-walled, rounded or pointed ear-like flap, flared to left, rolled over to right in uneverted penis; dorsal wall bearing about eight to 12 thin parallel ridges, alike in diameter, which is constant or gradually increases basally; ventral structures absent; peripheral step-like shoulder present or absent.

Shell: size medium to large (14-31 mm); shape **globose** (height/diameter, 0.6-0.7); umbilicus narrow, partly to fully and broadly covered; parietal denticle present and small, or absent; basal denticle absent; palatal denticle absent; periostracal hairs or scales absent.

Included species

Mesodon clausus (Say, 1821)
(Figs. 16b, 37c,d; Table 2; Fig. 52)

(1) Tennessee: Blount County (GS-9; FMNH 214643): 30 live adults, 30 tissue samples—electrophoresed #1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 15, 29. (2) Illinois: Carroll County (GS-19; FMNH 214644); ca. ten live adults, 16 tissue samples—electrophoresed #1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 13, 15. (3) Tennessee: Blount County [GS-28 (= GS-9); FMNH 214645]: one live adult-dissected #A, B, C, E. (4) Kentucky: Knox County (GS-116; FMNH 214650): 21 live adults, 21 tissue samples—dissected #6, 11, 17 (illustrated #11); illustrated shell #3. (5) Kentucky: Knox County [GS-188 (= GS-116); FMNH uncat.]: unknown number of live adults, unknown number of tissue samples—electrophoresed #1, 13.

Mesodon trossulus Hubricht, 1966
(Figs. 16c,37e,f; Table 2; Fig. 52)

(1) Alabama: Clarke County (GS-53; FMNH 214741); three live adults, five tissue samples—dissected #3 (illustrated); electrophoresed #1, 2, 3, 4, 5; illustrated shell #A.

Remarks. At its type locality *M. trossulus* was found sympatric with *M. clausus*—the shell of which not only lacked the color band, but also had a greener background color and a slightly different shape—without conchological intergradation. This variation in color might represent only a polymorphism; unfortunately live specimens of *M. clausus* were not found at the site for anatomical and electrophoretic tests.

Mesodon thyroidus (Say, 1817)
(Figs. 15b, 36c,d; Table 2; Fig. 52)

(1) Kentucky: Pulaski County (GS-13; FMNH 214743): ca. two live adults, ten tissue samples—electrophoresed #1, 2, 3, 4, 5, 6, 8, 9, 10. (2) Texas: Bastrop County (GS-63; FMNH 214744): ca. 12 live adults, 18 tissue samples—dissected #1, 6, 8, 14, 18 (illustrated #6); electrophoresed #1, 5, 7, 9, 10, 14; illustrated shell #11. (3) Texas: Trinity County (GS-74; FMNH 214750): ca. 40 live adults, 40 tissue samples—electrophoresed #2, 10. (4) Texas: Cherokee County (GS-78; FMNH 214751): ca. 20 live adults, 22 tissue samples—dissected #6, 8, 12; electrophoresed #12. (5) Illinois: Kane-Cook Counties (GS-207; FMNH uncat.): unknown number of live adults, unknown number of tissue samples—dissected #3; electrophoresed #3, 4.

APPENDIX 2. ALTERNATIVE PHYLOGENETIC ANALYSIS USING SUCCESSIVE WEIGHTING.

An alternative approach is Farris's (1988) method of successive weighting. This method first produces a set of maximum-parsimony trees, assigns each character a weight (0-10) according to its fit to these trees, reruns the analysis using the assigned weights, reweights each character according to the resulting trees, and iterates this process until the character-weights stabilize. "Successive weighting has the advantage of providing a means of basing groupings on more reliable characters without making prior decisions on weighting" (Farris, 1988).

Application of successive weighting to the data set (Table 4, but with a single change:

removal of the convergence in the dorsal ridge from *Patera appressa*) resulted in 1077 equally parsimonious trees, the strict consensus of which is presented in Figure 53.

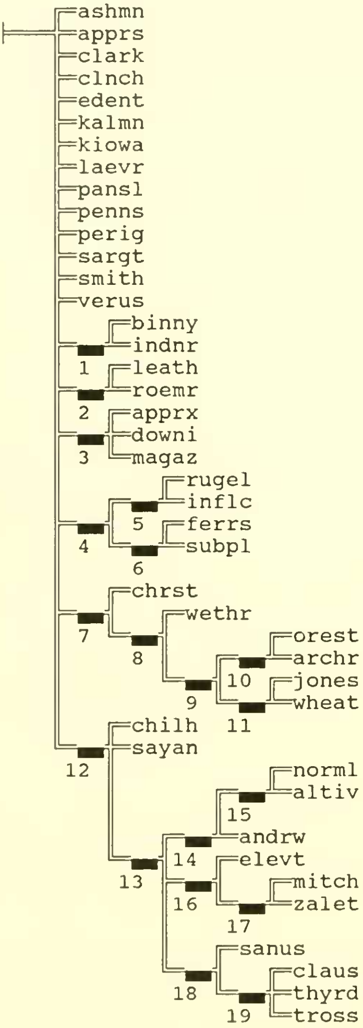

FIG. 53. Nelson consensus tree of 1077 maximum-parsimony cladograms generated from data matrix in Table 4, using successive-weighting algorithm of Hennig86. Character-state changes (numbers refer to Table 3) at each number in the cladogram are: 1. 50; 2. 7, 67, 71, 86(loss); 3. 0, 1, 25; 4. 2, 25; 5. 38, 87; 6. 3; 7. 10, 54; 8. 11; 9. 12, 16, 25, 50; 10. 5; 11. 4; 12. 13; 13. 18; 14. 14; 15. 37; 16. 19, 85; 17. 37, 57, 58(loss); 18. 15, 20; 19. 57, 58(loss), 72. This tree is very similar to, but not identical with, the preferred consensus tree (Fig. 52), which was used for taxonomic revision (Appendix 1).

APPENDIX 3.
ALTERNATIVE PHYLOGENETIC ANALYSIS TREATING GENITALIC AND ELECTROPHORETIC DATA SEPARATELY, THEN SEEKING A CONSENSUS.

Methods

Throughout this appendix, all subgeneric and generic assignments are those of Pilsbry (1940), and do not conform with the revised taxonomy arrived at in this paper (see Table 6). The analytical procedure used in this appendix was the same as that developed for the Triodopsini (Emberton, 1988). The procedure is summarized in Figure 54, and is described below.

Data for genitalic character states (Table 1) were analyzed cladistically by the Wagner criterion of unrestricted parsimony (Kluge & Farris, 1969; Farris, 1970), using the global branch-swapping algorithm in Swofford's (1983) PAUP program. The resulting single most parsimonious cladogram was designated the Anatomy Tree.

Allozyme data (Table 2) were subjected to both cladistic and phenetic analysis. The Triodopsini (Emberton, 1988) were used as the outgroup. Alleles not shared with the Triodopsini were considered apomorphic for maximum-parsimony analysis using the independent alleles model (Michevich & Johnson, 1976). The first 50 trees generated by PAUP (Swofford, 1983), using global branch-swapping, were compared branch by branch to determine the most frequent configuration of each branch. The resulting consensus cladogram was designated the Alleles Tree.

For phenetic analysis, the electrophoretic data were divided into two subsets. The first (Table 2, *M. altivagus* to *Ashmunella danielsi*) consisted of 38 species, one population each, with complete data for all 16 loci (total 88 alleles). The second subset (Table 2, *M. altivagus*—2 to *M. zaletus*—2) consisted of 37 populations representing 23 species (all but one of these species, *Inflectarius verus,* were the same as those of the first subset); in this second subset, all loci with partly missing data (Me, Gd-1, Gd-2, Sod-2) were omitted, leaving 12 loci (total 78 alleles) for the analysis. In each of the two subsets, the same population of *Ashmunella danielsi dispar* was included as outgroup. Separate distance-Wagner trees (Farris, 1970), with branch-length optimization, were computed from the Prevosti genetic distance matrix of each data subset, using NT-

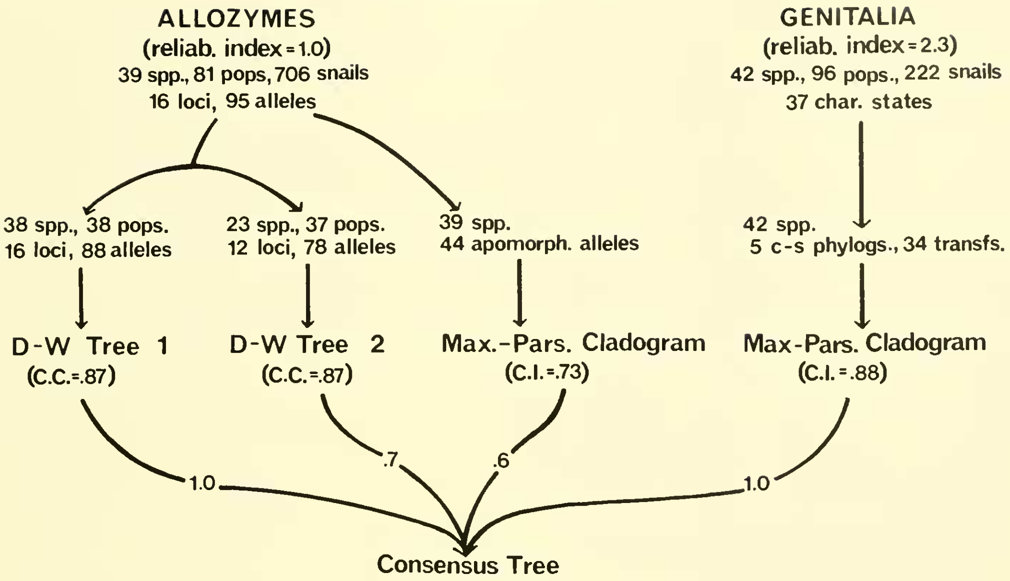

FIG. 54 Diagram of alternative procedure for phylogenetic analysis applied in Appendix 3. D-W Tree 1 = Wagner-1 Tree (Fig. 58); D-W Tree 2 = Wagner-2 Tree (Fig. 59); Max.-Pars. Cladogram (from allozymes) = Alleles Tree (Figs. 56, 57); Max.-Pars. Cladogram (from genitalia) = Anatomy Tree (Fig. 55); and Consensus Tree = Consensus Tree (Fig. 60). See Appendix 3 for explanation.

SYS (Rohlf et al., 1972). These trees were designated the Wagner-1 Tree and the Wagner-2 Tree, respectively, for purposes of comparison with the other two trees.

The four trees (Anatomy, Alleles, Wagner-1 and Wagner-2) were compared, branch by branch, to arrive at a Consensus Tree. Discrepancies among trees were resolved by invoking their weights. The weight of each tree (Fig. 54) was calculated as the number of data units (alleles or transformations) used in its construction, times the reliability index of its data units. The reliability of anatomical with respect to electrophoretic data was estimated by dividing the number of homoplasies and reversals in the Anatomy Tree by the number of homoplasies and reversals in the Alleles Tree. This method, although arbitrary, is at least objectively calculated.

Results

Anatomy Tree. To simplify the analysis, species were pooled that were identical in their distributions of the 34 transformations of the genitalic character states (Table 1). This procedure reduced the number of operational taxa from 42 species to 24. Eighteen of these groups consisted of a single species (*inflectus, ferrissi, smithi, pennsylvanicus, wetherbyi, christyi, wheatleyi, jonesianus, archeri, orestes, normalis, andrewsae, elevatus, zaletus, mitchellianus, thyroidus, altivagus* and *appressus*). Each of the six remaining species groups was temporarily named for one of its better-known species, regardless of prior generic and subgeneric placement. By far the largest of these groups was the *perigraptus* group, containing 12 species (*perigraptus, panselenus, sargentianus, laevior, clarki, indianorum, binneyanus, clenchi, kiowaensis, edentatus, verus* and *kalmianus*), as well as the outgroups. The *approximans* group had three species (*approximans, magazinensis* and *downieanus*); the *rugeli* group had two species (*rugeli* and *subpalliatus*); the *roemeri* group had two species (*roemeri* and *leatherwoodi*); the *sayanus* group had two species (*sayanus* and *chilhoweensis*); and the *clausus* group had three species (*clausus, trossulus* and *sanus*).

Maximum-parsimony analysis of these 24 taxonomic units, using the global branch-swapping option of PAUP (Swofford, 1983), resulted in a single most parsimonious tree (Fig. 55). This tree, hereafter called the Anat-

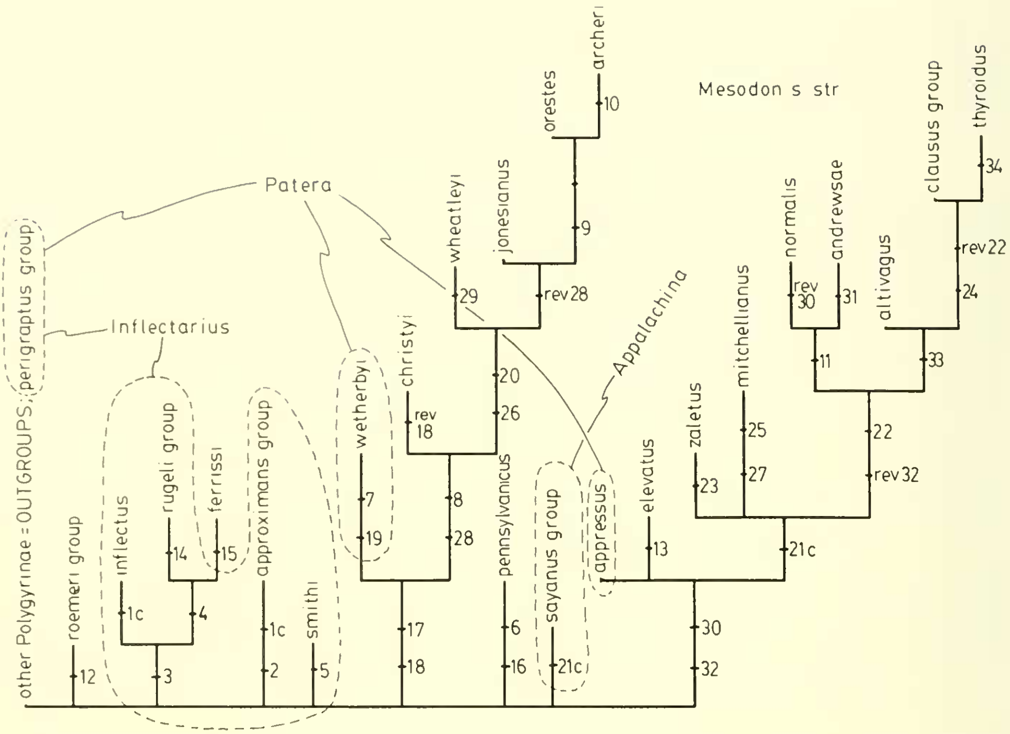

FIG. 55. Anatomy Tree: a phylogenetic hypothesis for the Mesodontini based on penial morphology (34 character-state transformations shown in Figs. 26–28). This is the single most parsimonious tree generated by PAUP, with a consistency index of 0.882.

omy Tree, had two homoplasies (Transformations 1 and 21) and six reversals (Transformations 8, 18, 22, 28, 30 and 32), giving an overall consistency index of 0.882. None of these homoplasies and reversals seemed biologically impossible. The two homoplasies and four of the reversals (Transformations 18, 22, 30 and 32) were seemingly robust. The reversals in Transformations 8 and 28, however, could be obviated fairly parsimoniously by moving the *jonesianus-orestes-archeri* branch from its dichotomy with *wheatleyi* to a trichotomy with *wetherbyi* and a *christyi-wheatleyi* branch. This alternative substituted reversals in Transformations 8 and 28 for homoplasies in Transformations 8, 20 and 26, thereby slightly reducing the overall consistency index from 0.882 to 0.868. Because homoplasies in Transformations 20 and 26 seemed biologically unlikely, there was no good reason for choosing this less parsimonious alternative. Thus, Figure 55 shows the best cladogram to fit the suggested transformations (Figs. 26-28). The branch lengths of this Anatomy Tree were scaled to the number of transformations they contain and are therefore approximate indicators of the degrees of evolutionary change.

Alleles Tree. Forty-four, or 46%, of the 95 alleles detected in the Mesodontini (Table 2) were not detected in the Triodopsini and were therefore presumed to be apomorphic. These alleles are listed in Table 9, along with their distributions among the species of the Mesodontini. Twenty-seven of these alleles were restricted to a single species, and each of the remaining 17 alleles was present in two to 14 species.

Maximum-parsimony analysis of the data in Table 9 produced the cladogram shown in Figure 56. This tree, henceforth called the Al-

TABLE 9. Allozyme alleles presumed apomorphic in the Mesodontini (i.e., undetected in their outgroup, the Triodopsini) and the species in which they were detected.

1.	Sordh$_{97}$	clausus, perigraptus
2.	Mdh-1$_{99}$	approximans, edentatus, ferrissi, inflectus, magazinensis, rugeli, smithi, subpalliatus, verus, wheatleyi
3.	Mdh-1$_{95}$	edentatus, kalmianus
4.	Mdh-1$_{90}$	thyroidus
5.	Me$_{101}$	chilhoweensis, sayanus, thyroidus
6.	Icd$_{110}$	clarki
7.	Icd$_{106}$	clarki, ferrissi, subpalliatus, thyroidus
8.	Icd$_{105}$	sanus
9.	Icd$_{97}$	christyi
10.	Icd$_{95}$	rugeli
11.	Pgd$_{103}$	clarki
12.	Gd-1$_{104}$	inflectus, rugeli
13.	Gd-1$_{100}$	altivagus, zaletus
14.	Sod-1$_{107}$	laevior
15.	Sod-1$_{105}$	leatherwoodi
16.	Sod-1$_{102}$	panselenus
17.	Sod-2$_{110}$	andrewsae, ferrissi
18.	Sod-2$_{104}$	zaletus
19.	Sod-2$_{101}$	subpalliatus, wetherbyi
20.	Sod-2$_{89}$	sayanus
21.	Got-1$_{110}$	leatherwoodi
22.	Got-1$_{103}$	andrewsae, chilhoweensis, clarki, clausus, kalmianus, mithcellianus, orestes, pennsylvanicus, roemeri, sanus, sayanus, thyroidus, trossulus, zaletus
23.	Got-1$_{101}$	christyi, orestes, wetherbyi, wheatleyi, zaletus
24.	Got-1$_{94}$	verus
25.	Got-1$_{90}$	kiowaensis
26.	Got-2$_{104}$	panselenus
27.	Got-2$_{98}$	sayanus
28.	Got-2$_{94}$	panselenus, wheatleyi
29.	Pgm$_{106}$	sargentianus
30.	Pgm$_{105}$	approximans
31.	Pgm$_{101}$	perigraptus
32.	Pgm$_{96.5}$	thyroidus
33.	Pgm$_{95.5}$	ferrissi
34.	Pgm$_{92}$	leatherwoodi, roemeri, rugeli
35.	Pgm$_{90}$	subpalliatus
36.	Pgm$_{89}$	roemeri
37.	Lap$_{104}$	andrewsae
38.	Lap$_{93}$	appressus, clarki, edentatus, inflectus, kalmianus, smithi
39.	Mpi$_{97}$	ferrissi
40.	Gpi$_{105}$	andrewsae, chilhoweensis, leatherwoodi, orestes, perigraptus, roemeri, sanus
41.	Gpi$_{103}$	elevatus, mitchellianus, thyroidus, zaletus
42.	Gpi$_{101}$	kalmianus
43.	Gpi$_{97}$	sayanus
44.	Gpi$_{96}$	inflectus, rugeli, smithi

leles Tree, represents the plurality consensus (see below) of the first 50 of an unknown number of equally parsimonious cladograms generated by the global branch-swapping option of PAUP. In the Alleles Tree, homoplasies occurred in 14 of the 44 alleles [numbers 1, 2 (twice), 3, 5, 7, 13, 17, 19, 22, 23, 28, 34, 40 (twice), and 41]; reversals occur in five of the 44 alleles [numbers 7, 22 (twice), 23, 38 (thrice), and 40]; and 28 of the 44 alleles occurred without homoplasy or reversal.

To aid discussion, various branches of the Alleles Tree are labeled A through K in Figure 56. Branches A, B, C, E and F were stable in all of the 50 trees examined, and branch D occurred in the Alleles Tree in 49, or 98%, of the 50 trees. The remaining branches (G-K) occurred in the Alleles Tree more commonly than any alternative, and were represented in 32% to 94% of the 50 trees (Fig. 57). Figure 57 lists the alternative configurations of branches G-K, introduces the additional minority branch L and lists the alternative topologies of the Alleles Tree itself.

Distance-Wagner Trees. The two subsets of allozyme data were analyzed using BIOSYS (Swofford & Selander, 1981). Prevosti distance matrices (Emberton, 1986: Appendices C-1, C-2, available from the author upon request) were calculated, then subjected to the distance-Wagner procedure with branch-length optimization, producing the two trees shown in Figures 58 and 59.

The 38-species, complete-data tree (Wagner-1 Tree, Fig. 58) had a cophenetic correlation of 0.866, indicating only mild distortion of the original genetic distance matrix. The 23-species, 37-population, reduced-data tree (Wagner-2 Tree, Fig. 59) had a similarly high cophenetic correlation of 0.872.

Consensus Tree. In the Anatomy Tree (Fig. 55), eight homoplasies and reversals oc-

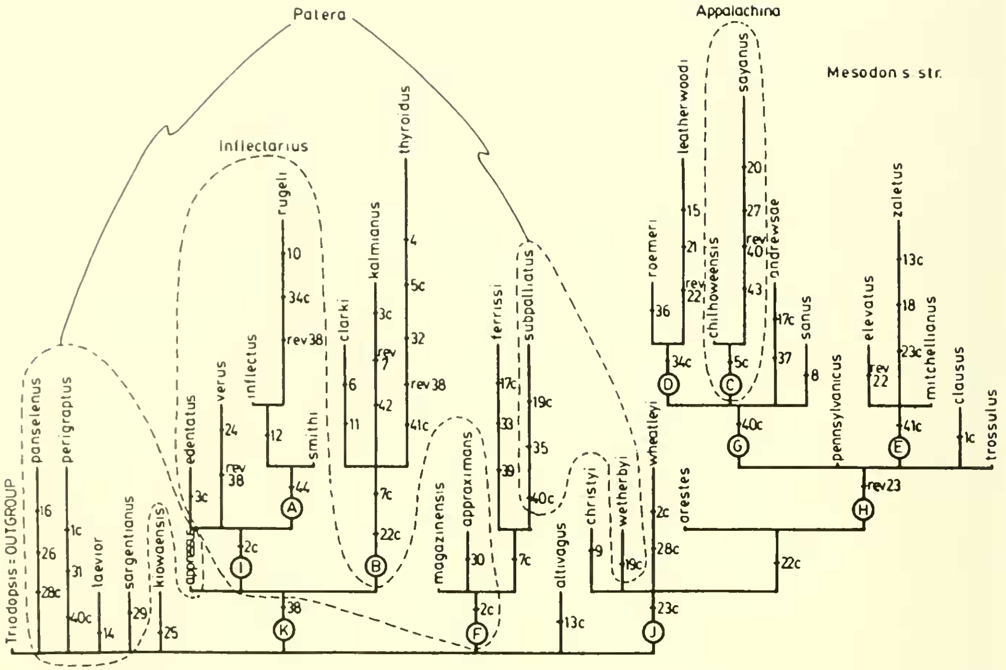

FIG. 56. Alleles Tree: a phylogenetic hypothesis for the Mesodontini based on allozymes, with Triodopsini as outgroup. The 44 presumed apomorphic alleles are listed in Table 9. This tree is the plurality consensus of 50 trees of equal and maximal parsimony generated by PAUP. Gender endings conform to Pilsbry's usage (1940); revised endings shown in Table 6.

curred among the 34 transformations (ratio 0.24, rounded to two decimal places), and in the Alleles Tree (Fig. 56), 24 homoplasies and reversals occurred among the 44 transformations (ratio 0.55, rounded to two decimal places); thus the reliability index for anatomical with respect to electrophoretic data is 2.32 (rounded to two decimal places). The Wagner-1 Tree (Fig. 58) was based upon 88 electromorphs, and the Wagner-2 Tree (Fig. 59) was based upon 78 electromorphs. Thus the Anatomy, Alleles, Wagner-1 and Wagner-2 Trees were constructed from the following numbers of roughly equivalent data units, respectively: 78.9 (i.e., 34 × 2.32), 44, 88 and 62. After multiplying the values for the two Wagner Trees by their respective cophenetic correlations to adjust for their distortion of the original distance data (this is an additional calculation not performed in the Triodopsini analysis of Emberton, 1988), the results were divided by 78.9 and rounded to get the following relative weights:

Anatomy Tree	1.0
Alleles Tree	0.6
Wagner-1 Tree	1.0
Wagner-2 Tree	0.7

These weights are shown within the bottom arrows in Figure 54, which summarizes the procedure used for this analysis. The trees then were compared visually, branch by branch, to arrive at a consensus tree, using the weights to resolve discrepancies.

To aid comparisons among Trees, three of the four subgenera of the Mesodontini recognized by Pilsbry (1940), *Patera, Inflectarius* and *Appalachina,* were delimited by dashed lines; all species and species groups were members of Pilsbry's fourth subgenus, *Mesodon s. str.* (Figs. 55-59). It is apparent in the four Trees (Figs. 29-33) that not all of these four nominal subgenera are discrete and coherent. *Appalachina* is the only one that seems not to require modification from Pilsbry's concept. This subgenus is equivalent to

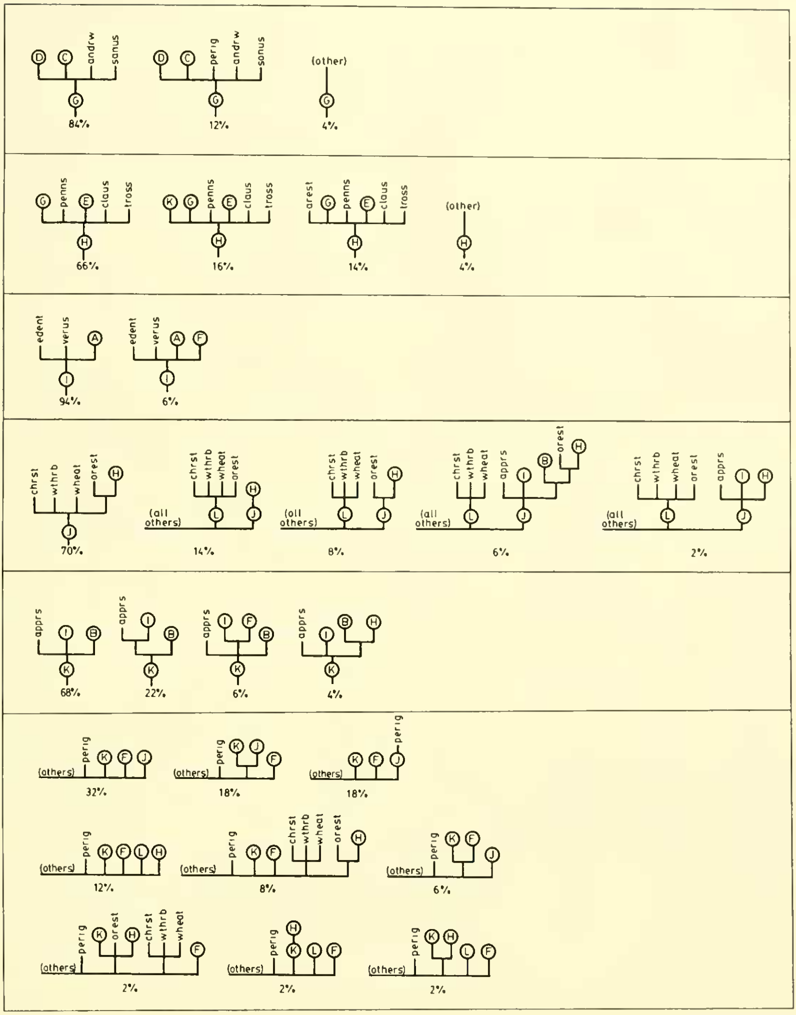

FIG. 57. Alternative topologies of Alleles Tree (Fig. 56), of equal parsimony and among the first 50 trees generated by PAUP.

the *sayanus* group; its two species (*sayanus* and *chilhoweensis*) are tightly linked and isolated in the Anatomy and Alleles Trees (total weight, 1.6) and are closely linked, in combination with *clausus, trossulus* and *thyroidus,* in the Wagner-1 Tree (weight, 1.0). These linkages easily outweigh the separation of *sayanus* and *chilhoweensis* in the Wagner-2 Tree (weight, 0.7).

Pilsbry's (1940) subgenus *Inflectarius* is strongly supported by the Wagner-1 and Wagner-2 Trees (Figs. 32, 33; total weight, 1.7); less strongly supported by the Alleles Tree (Fig. 30; weight, 0.6), and weakly supported, with some members combined with *Patera* and some *Mesodon s. str.* in the *perigraptus* anatomical group, in the Anatomy Tree (Fig. 29; weight, 1.0). The combined weight of the evidence supports two conclusions: that *Inflectarius* is a coherent monophyletic group, and that it must be expanded to include *M.* (*Mesodon*) *ferrissi* and *M.* (*Patera*) *subpalliatus.* The pairing of *ferrissi* and *subpalliatus* as a lineage within *Inflectarius* occurs in the Anatomy Tree (with *subpalliatus* a member of the *rugeli* group), in the Alleles Tree and in the Wagner-2 Tree; only *ferrissi* occurs in this position in the Wagner-1 Tree,

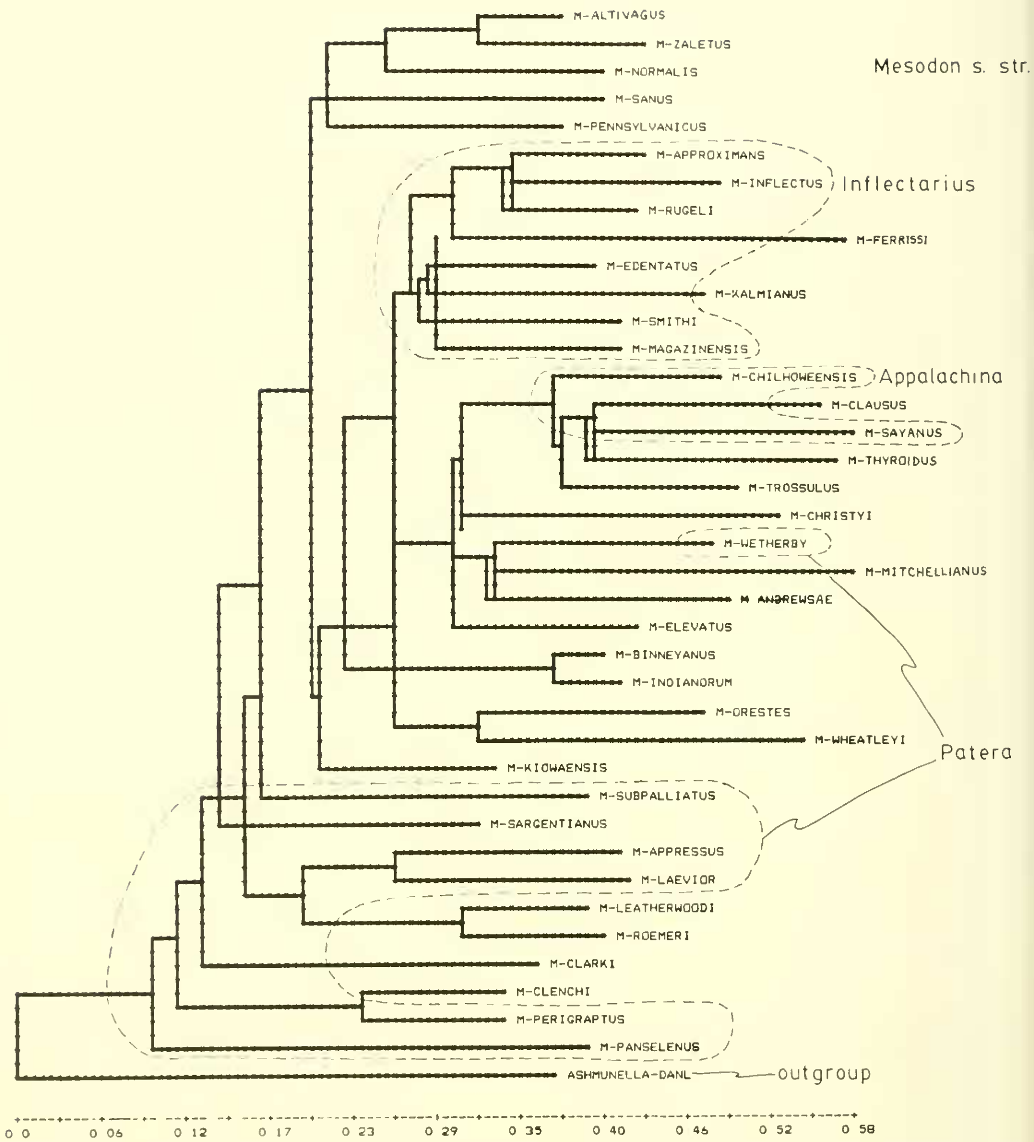

FIG. 58. Wagner-1 Tree: distance-Wagner tree for 38 species of Mesodontini, with *Ashmunella* as outgroup. Computed from Prevosti distance matrix based on 16 allozyme loci (Table 2, upper half). Cophenetic correlation is 0.866; branch lengths are optimized. Gender endings conform to Pilsbry's usage (1940); revised endings shown in Table 6.

in which *subpalliatus* is well separated, but this separation is outweighed (2.3 to 1.0) by the position of *subpalliatus* in the other three trees. *M.* (*Mesodon*) *kalmianus* also seems to belong in *Inflectarius*: not only does it have penial morphology indistinguishable from that of *edentatus* (both are in the *perigraptus* anatomical group), but also it clusters closest to *edentatus* in the Wagner-1 Tree. In the Alleles Tree *kalmianus* also occurs within *Inflectarius*; it was not included in the Wagner-2 Tree. One other member of Pilsbry's *Mesodon s. str., downieanus*, seems to belong to *Inflectarius* because of its apparent membership in

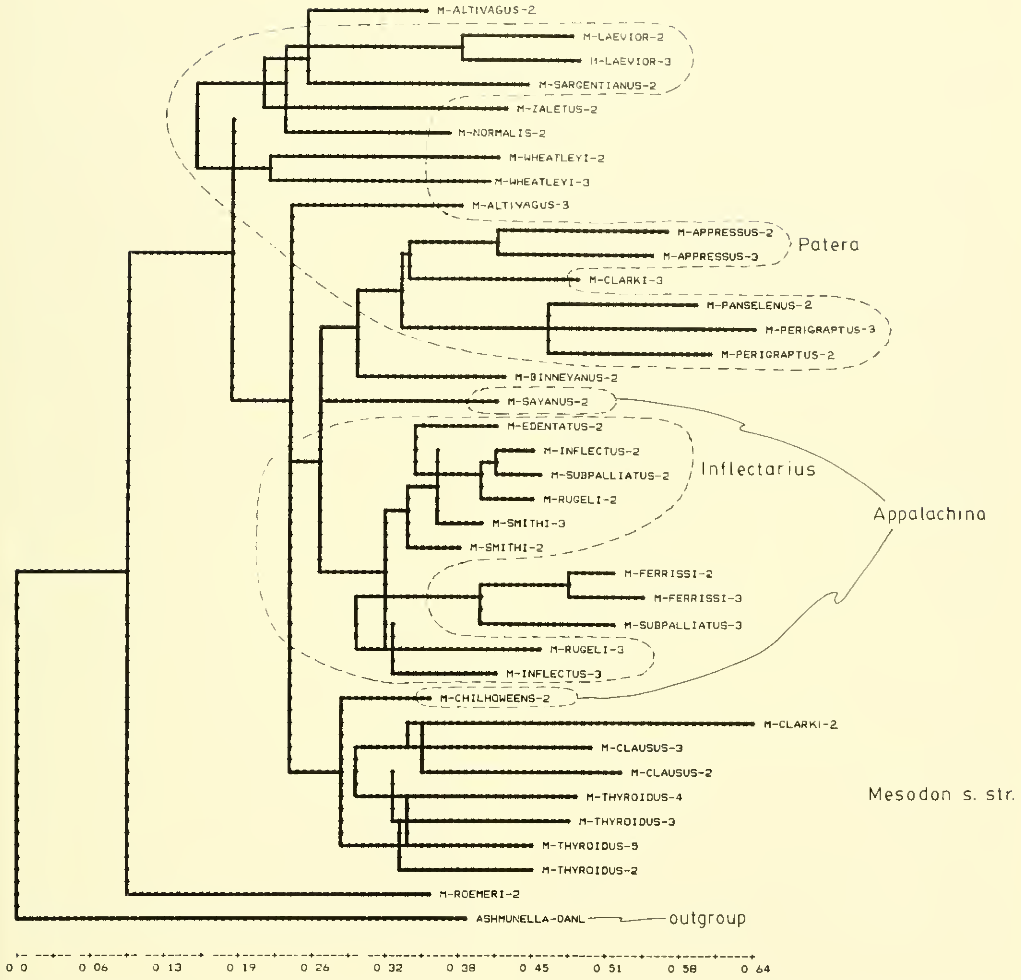

FIG. 59. Wagner-2 Tree: distance-Wagner tree for one additional species and 29 additional populations of 22 of the species of the Mesodontini represented in Wagner-1 Tree (Fig. 58), with *Ashmunella* as outgroup. Computed from Prevosti distance matrix based on 12 allozyme loci for which all populations had complete data (Table 2, lower half). Cophenetic correlation is 0.872; branch lengths are optimized. Gender endings conform to Pilsbry's usage (1940); revised endings shown in Table 6.

the *approximans* anatomical group. Unfortunately, because electrophoretic data were not available, the position of *downieanus* is highly problematic; nevertheless it is tenatively transferred to *Inflectarius* on the basis of its penial morphology.

Pilsbry's (1940) subgenus *Patera* seems to be a coherent group, both anatomically and electrophoretically, requiring expansion to include *M.* (*Mesodon*) *clarki* and Pilsbry's *binneyanus* group (*binneyanus, indianorum, clenchi, kiowaensis, roemeri* and *leatherwoodi*), also of *Mesodon s. str.;* and requiring the removal of two species, *subpalliatus* and *wetherbyi*. The removal of *subpalliatus* to *Inflectarius* was justified above. Tentative removal of *wetherbyi* from *Patera* to *Mesodon s. str.* is based upon its clear and consistent isolation from that subgenus in the Anatomy, Alleles and Wagner-1 Trees (*wetherbyi* was not included in the Wagner-2 Tree). Removal of *clarki* to *Patera* is indicated by its membership in the *perigraptus* anatomical group, by its clustering within *Patera* in the Wagner-2 Tree and by the clustering of one of its two populations within *Patera* in the Wagner-2 Tree. The combined weight of these positions in trees [1.0 + 1.0 + (0.5)(0.7) = 2.35] strongly outweights the combined weight of the Alleles Tree and of one of the two populations in the Wagner-2 Tree [0.6 + (0.5)(0.7) = 0.95], in which *clarki* appears outside *Patera*. Transferral of Pilsbry's *binneyanus* group to *Patera* is indicated by the membership of *binneyanus, indianorum, clenchi* and *kiowaensis* in the *perigraptus* anatomical group, (which also includes all of *Patera* except *appressus*) by the separation of *roemeri* and *leatherwoodi* from this anatomical group by a single transformation (Transformation 12; Fig. 29); by the clustering of *roemeri, leatherwoodi* and *clenchi* within *Patera* and of *kiowaensis, binneyanus* and *indianorum* adjacent to or very close to *Patera* in the Wagner-1 Tree (Fig. 32); and by the clustering of *binneyanus* within *Patera*, and of *roemeri* very close to *Patera* in the Wagner-2 Tree, in which these two species are the sole representatives of the *binneyanus* group. This conclusion is also supported by the Alleles Tree, in which *kiowaensis* is the only member of Pilsbry's *binneyanus* group to appear because all of its other members lack derived alleles (Table 9); *kiowaensis* thus shares a basal position in the Alleles Tree with most members of *Patera* (minus *subpalliatus* and *wetherbyi*, and plus *clarki*).

Species not included in *Appalachina*, in the modified *Inflectarius*, or in the modified *Patera*, are assigned temporarily to *Mesodon s. str.* by default. Each of these four nominal subgenera are treated in turn, from the most plesiomorphic to the most apomorphic, with discussion of the evidence of the four Trees (Figs. 55-59) concerning its affinities and the evolutionary relationships of its component species.

Patera, as modified above, is clearly the most plesiomorphic subgenus of the Mesodontini. It occupies the basal position in the Anatomy Tree (Fig. 55), the Alleles Tree (Figs. 56, 57), the Wagner-1 Tree (Fig. 58) and the Wagner-2 Tree (Fig. 59).

Penial morphology is of little use in determining evolutionary relationships within *Patera*, because only two derived character states (Transformations 12, 30-32) occur within it. This latter character state, homoplasious with Transformations 30 and 32 in a subset of *Mesodon s. str.* (Fig. 29), is unique to *appressus*. Transformation 12, however, links *roemeri* and *leatherwoodi* (the *roemeri* anatomical group). This *roemeri* group is also tightly linked in the Wagner-1 Tree, the only other Tree in which both these species occur, and therefore constitutes the most robust affinity within *Patera*.

The Alleles Tree is also unhelpful concerning *Patera;* it does not show any links among its species.

The tight linkage between *perigraptus* and *clenchi* in the Wagner-1 Tree is suspect. The single specimen of "*clenchi*" that was electorphoresed was a juvenile from a site (GS-97) at which *perigraptus* was common. Because juveniles of these two species are very difficult to distinguish, the electrophoresed specimen of *clenchi* in Table 2 and Figure 58 might actually be a specimen of *perigraptus*.

In the Wagner-2 Tree, *panselenus* links to *perigraptus* at the same level as the two populations of *perigraptus*. This linkage is supported by the adjacent positions of *panselenus* and *perigraptus* in the Wagner-1 Tree, and is therefore relatively robust.

The linkage of *binneyanus* and *indianorum* in the Wagner-1 Tree is so tight that there can be little doubt that they are sister species. There is no test of this linkage in the Wagner-2 Tree, however, because *indianorum* was not included in it.

The linkage of *appressus* and *laevior* in the Wagner-1 Tree (weight, 1.0) slightly outweighs their separation in the Wagner-2 Tree (weight, 0.7). The consensus of these two trees seems best expressed as a trichotomy among *appressus, laevior* and *sargentianus*, because *sargentianus* appears at the base of the *appressus-laevior* branch in the Wagner-1 Tree and paired with *laevior* (two populations) in the Wagner-2 Tree.

The consensus of the two Wagner Trees also seems to support a trichotomy among the *panselenus-perigraptus* branch, the *appressus-laevior-sargentianus* branch and *clarki*. This pattern is approximately that remaining in the lower portion of the Wagner-1 Tree upon removal of the *roemeri-leatherwoodi* branch and it is the pattern present in the middle portion of the Wagner-2 Tree upon removal of the *laevior-sargentianus* branch to a trichotomy with *appressus*, as discussed above.

The reason for removing the *roemeri-leatherwoodi* branch from the trichotomy just discussed is the very different position of *roemeri* in the Wagner-2 Tree. In this tree, from which *leatherwoodi* is absent, *roemeri* is the most primitive species of the entire genus and, although linked to the remainder of *Patera*, lies well outside it. The two Wagner Trees also differ in the position of the *binneyanus-indianorum* branch. In the Wagner-1 Tree, this branch, along with *kiowaensis,* lies within *Mesodon s. str.,* fairly well isolated (but perhaps not significantly so) from the rest of *Patera.* In the Wagner-2 Tree, however, this branch (represented by *binneyanus* only) appears as a sister-group of the *appressus-clarki-panselenus-perigraptus* branch. The best resolution of these differences seems to be the topology for *Patera* presented in the Consensus Tree, in which *kiowaensis* is linked to the base of the *binneyanus-indianorum* branch, and in which this branch joins that of *roemeri-leatherwoodi.* Owing to the high probability of misidentification of the "*clenchi*" tissue sample, noted earlier, *clenchi* is tentatively placed with *kiowaensis* in recognition of their very great conchological similarity.

Inflectarius, as modified above, seems to be most closely allied to the revised *Patera* because three of its members (*edentatus, verus* and *kalmianus*) are in the *perigraptus* anatomical group, and because its other members show relatively limited derivation beyond this primitive kind of penial morphology (Anatomy Tree, Fig. 55). Analyses of the electrophoretic data (Figs. 56-59) together weakly support this alliance with *Patera.* In the Alleles Tree, three members of *Patera* (*appressus, clarki* and *kalmianus*) appear within *Inflectarius,* whereas none of its members appear within either *Appalachina* or *Mesodon s. str.* In the Wagner-2 Tree, *Inflectarius* clusters in a trichotomy with most species of *Patera* and one of the two species of *Appalachina.* In the Wagner-1 Tree, one member of *Inflectarius* (*subpalliatus*) clusters just above the most of *Patera,* and the rest of *Inflectarius* clusters just above three members of *Patera* (*binneyanus, indianorum* and *kiowaensis*), although at the same level as various members of *Mesodon s. str.* and *Appalachina.*

The relatively robust linkage between *ferrissi* and *subpalliatus* was discussed above.

A close linkage between *inflectus* and *rugeli* occurs in all four Trees. In the Wagner-1 Tree, *inflectus* and *rugeli* form a trichotomy with *approximans;* this trichotomy is accepted in the Consensus Tree (Fig. 60), because the *approximans* group and *inflectus* can be paired in the Anatomy Tree without change in the consistency index (exchanging a homoplasy in Transformation 1 for a reversal in Transformation 3), and because *approximans,* along with *magazinenesis* and the *ferrissi-subpalliatus* branch, can be approximated to the *inflectus-rugeli-smithi* branch in the Alleles Tree without change in the consistency index (exchanging a homoplasy in Transformation 2 for a reversal in Transformation 38); *approximans* was not included in the Wagner-2 Tree.

The relationship of *verus* to this *inflectus-rugeli-approximans* trichotomy is problematic. In the Wagner-2 Tree, *verus* pairs tightly with one population of *inflectus;* in the Anatomy Tree, *verus* groups with *edentatus* and *kalmianus* in the primitive *perigraptus* anatomical group. In the Alleles Tree, *verus* appears in two equally parsimonious trichotomies, both having one branch consisting of *edentatus* and a second branch comprising *inflectus, rugeli* and *smithi*; the third branch consists of either *verus* alone or *verus* together with *approximans, magazinensis* and the *ferrissi-subpalliatus* branch. As a reasonable resolution of these different positions, *verus* is placed in a dichotomy with the *inflecus-rugeli-approximans* branch in the Consensus Tree.

Placement of the *ferrissi-subpalliatus* branch clearly should be within or near the *verus-inflectus-rugeli-approximans* branch. In the Anatomy Tree, as modified above from Figure 55, the *ferrissi-subpalliatus* branch, along with *rugeli,* forms a dichotomy with the *inflectus-approximans* group branch. In the Alleles Tree, as modified above from Figure 56, the *ferrissi-subpalliatus* branch arises from a branch on the same level with *verus* and *approximans,* although also with *magazinensis.* In the Wagner-1 Tree (Fig. 58), *ferrissi* clusters at the base of the *inflectus-rugeli-approximans* branch. In the Wagner-2 Tree as well (Fig. 59), the *ferrissi-subpalliatus* branch arises between two populations each of *inflectus* and *rugeli,* although sharing this position with *smithi* and *edentatus.* The best consensus of these topologies seems to be that expessed in the Wagner-1 Tree, with the addition of *verus:* thus the *ferrissi-subpalliatus* branch in the Consensus Tree (Fig. 60) forms a dichotomy with the *verus-inflectus-rugeli-approximans* branch.

The position of *edentatus, magazinensis* and *smithi* in the Wagner-1 Tree basal to the *verus-inflectus-ferrissi* lineage, discussed above, is supported both by their basal, although slightly separated, positions in the modified Alleles Tree, and by the basal positions of *edentatus* (as a member of the *perigraptus* anatomical group) and *smithi*—although not of *magazinensis*—in the Anatomy Tree, but is slightly contradicted by the clus-

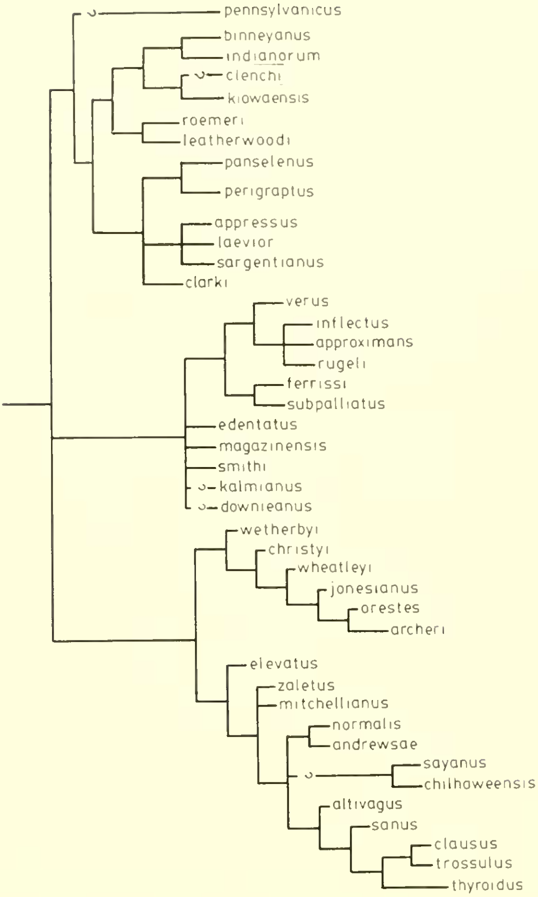

FIG. 60. Consensus Tree: alternative phylogenetic hypothesis for the Mesodontini, representing weighted consensus of Anatomy, Alleles, Wagner-1, and Wagner-2 Trees (Figs. 55–59). This tree is very similar to, but not identical with, preferred consensus tree (Fig. 52), which was used for taxonomic revision (Appendix 1). Gender endings conform to Pilsbry's usage (1940); revised endings shown in Table 6.

tering of *edentatus* and *smithi* between populations of *inflectus* and *rugeli,* and on about the same level as the *ferrissi-subpalliatus* branch in the Wagner-2 Tree (Fig. 59). In view of the weights of these trees, the consensus topology seems to be with *edentatus, magazinensis* and *smithi* arising at the same level, basal to the *verus-inflectus-ferrissi* lineage.

The position of *kalmianus* is somewhat problematic. It shares a primitive penial morphology with *edentatus* and *verus* (*perigraptus* group in the Anatomy Tree), and it clusters with *edentatus, magazinensis* and *smithi* in the Wagner-1 Tree, but it is fairly isolated and highly derived in the Alleles Tree (*kalmianus* was not included in the Wagner-2 Tree). The best compromise, in view of the weights of the three trees, seems to be with *kalmianus* arising at the same level as *edentatus, magazinensis* and *smithi* as shown in the Consensus Tree.

The position of *downieanus* in *Inflectarius* is highly problematic owing to the lack of electrophoretic data and the uncertainty about its penial morphology as a result of contractional distortion of the only specimens available for dissection. Its apparent, but questionable, membership in the *approximans* anatomical group, which includes *approximans* and *magazinensis,* is unindicative of its topological position in the Consensus Tree. Therefore *downieanus,* marked with question marks, is tentatively placed at the basal level of *Inflectarius.*

Pilsbry's (1940) *Mesodon s. str.* seems to be a catch-all subgenus for those species with globose shells and minimal apertural dentition. *Mesodon s. str.* was already reduced in the present analysis by removing *kalmianus* and *downieanus* to *Inflectarius,* and is further expanded here by transferring *wetherbyi* from *Patera.* The Anatomy Tree indicates discrete clusters within *Mesodon s. str.* One of these anatomically differentiated groups (*wetherbyi, christyi, wheatleyi, jonesianus, orestes* and *archeri*), henceforth called the *wheatleyi* group, is at least partly validated in two of the three electrophoretic trees. In the Alleles Tree the four electrophoresed species of the *wheatleyi* group (*wetherbyi, christyi, wheatleyi* and *orestes*) group together either at the base of the rest of *Mesodon s. str.* (of Pilsbry, 1940) (Fig. 56; Fig. 57, left-most topology of "J") or as an independent branch (branch "L"). In the Wagner-1 Tree, *wheatleyi* and *orestes* cluster together, and *wetherbyi* and *christyi* cluster near each other and slightly removed from the *wheatleyi-orestes* branch. Only *wheatleyi* (two populations) occurs in the Wagner-2 Tree. Because of this validation in the other two allozymal trees, I have adopted unchanged in the Consensus Tree the topology of the *wheatleyi* group in the Anatomy Tree.

Among the remaining species of *Mesodon s. str.*, a fairly robust group is that comprising *thyroidus* and the *clausus* anatomical group (*clausus, trossulus* and *sanus*), henceforth called the *thyroidus* group. These four species are tightly clustered in the Anatomy Tree. In the Wagner-1 Tree, *thyroidus, clausus* and *trossulus* cluster closely (along with *Appalachina*), but *sanus* is remote; this isolation of *sanus* in the Wagner-1 Tree is counterbalanced, however, by its position in the Alleles Tree, in which *sanus* is separated from *clausus* and *trossulus* by only a single transformation (Transformation 40). The aberrant position of *thyroidus*—in a trichotomy with *clarki* and *kalmianus* within *Inflectarius*—in the Alleles Tree is counterbalanced by its consistent clustering with *clausus* (four and two populations respectively) in the Wagner-2 Tree. Thus the consensus of these trees seems to be the pairing of *clausus* and *trossulus* in a branch joining *thyroidus* to form a three-species branch joined to *sanus,* as shown in the Consensus Tree.

The anatomical uniqueness of *pennsylvanicus* is indisputable (see Transformations 6, 16) and is not contradicted by the position of this species in the Alleles and Wagner-1 Trees. Its position is unclear, but it is placed tentatively in this analysis at the base of *Patera.* The remaining six species of *Mesodon s. str.* (of Pilsbry, 1940) (*normalis, andrewsae, elevatus, zaletus, mitchellianus* and *altivagus*), are grouped in the Anatomy Tree along a single lineage leading to the *thyroidus* group. This topology is supported by the Wagner-1 Tree in that these six species appear primitive with respect to the *thyroidus* group, but seems to be contradicted in this tree in that these six species are split into two isolated clusters, the first one close to the majority of the *thyroidus* group and comprising *andrewsae, elevatus* and *mitchellianus,* and the second one distant from the majority of the *thyroidus* group and comprising *normalis, zaletus* and *altivagus.* This apparent contradiction, however, is counterbalanced by the fact that the latter, distant group does indeed cluster near one member of the *thyroidus* group (*sanus*); thus the parallel isolation of *sanus* and of the *normalis-zaletus-altivagus* cluster might be an idiosyncracy of the Wagner-1 Tree that distorts true relationships. This view is supported by the topology of the Alleles Tree, in which the six species are either all on an equivalent branch level, or are primitive to the *thyroidus* group and are separated, but into clusters different from those in the Wagner-1 Tree. The Wagner-2 Tree, although it differs from the other trees in intermixing the three of these six species that it includes (*altivagus, normalis* and *zaletus*) with *Patera* and with the *wheatleyi* group, supports the other trees in placing these species primitive to the *thyroidus* group. In addition, it shows a great distance between the two populations of *altivagus;* such high intraspecific variation (or cryptic species) might cause other discrepancies among the four trees with respect to the positions of all six species.

With regard to the interrelationships among these six species, I have chosen to follow the topology of the Anatomy Tree. The juxtaposition of *elevatus, zaletus* and *mitchellianus* in this Tree is mirrored by their trichotomy in the Alleles Tree. The clustering of *altivagus, normalis* and *zaletus* in both the Wagner-1 and Wagner-2 Trees approximately supports their proximity in the Anatomy Tree. The clustering of *elevatus, mitchellianus* and *andrewsae* in the Wagner-1 Tree likewise supports their relative positions in the Anatomy Tree. Owing to the isolated, contradictory position of *altivagus* in the Alleles Tree, and owing to the fact that its position in the Anatomy Tree depends upon tentative decisions about the homology of its dorsal ridges, a question mark appears on the position of this species in the Consensus Tree, which otherwise exactly duplicates the topology of the Anatomy Tree for *elevatus, zaletus, mitchellianus, normalis, andrewsae* and *altivagus*.

In phylogenetic position *Appalachina* (*sayanus* and *chilhoweensis*) is very close to the *thyroidus* group, according to the Wagner-1 Tree and, to a lesser extent, the Wagner-2 and the Alleles Trees. The consensus of these three trees (combined weight, 2.3) clearly outweighs the Anatomy Tree (weight, 1.0). In the Consensus Tree, therefore, *Appalachina* tentatively appears at the base of the *thyroidus* group and *altivagus* combined, a position that only slightly decreases the parsimony of its position in the Anatomy Tree by exchanging one homoplasy (in Transformation 21) for two reversals (in Transformations 30, 22).

The completed Consensus Tree for the Mesodontini is presented in Figure 60.